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ARTHROXYLON, A REDEFINED GENUS OF CALAMITE*

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During the investigation of a specimen of a calamitean stem from an American coal field (described below) its relationship to *Arthrodendron* Scott 1899 (*Calamopitus* Will. 1871) was discovered. However, the name *Arthrodendron* may not be employed now, because, as will be shown, it is invalid in this sense.

In his first accounts of this material Williamson (1871, 1871a) was convinced of: (1) the calamitean affinity of the specimens; and (2) the fact that they differed structurally from other calamitean stems with cellular preservation that had been described. Accordingly, he called the specimens *Calamopitus*. But as for a binary name, he wrote: "I am disposed to regard all specific names and definitions as worthless. They separate things that I believe to be identical, and confound others that are obviously distinct" (1871). After some consideration of the different structural types of calamitean stems, that is *Calamodendron* Brong. 1849, *Arthropitys* Goepp. 1864, and *Calamopitus* Will. 1871, Williamson and Scott (1894) concluded: "We think . . . . *Calamopitus* should be retained. Besides the peculiar structure of its medullary rays it is characterized by the predominance of reticulated elements in its wood."

Sometime later Seward (1898) explained the substitution of the term *Arthrodendron* for *Calamopitus* thus: "Williamson's name *Calamopitys*[1] had previously been made use of by Unger for plants which do not belong to the Calamarieae. As it is convenient to have some term to apply to such stems as those which Williamson made the type of *Calamopitys*, the name *Arthrodendron* is suggested by my friend Dr. Scott as a substitute for Williamson's genus." Farther along, Seward 1898) recognized and elaborated on the three structural types, or "sub-genera" as he called them, yet while he mentioned various species of both *Calamodendron* and *Arthropitys* there was no binomial for *Arthrodendron*.

[1]Seward here uses the orthographic form.

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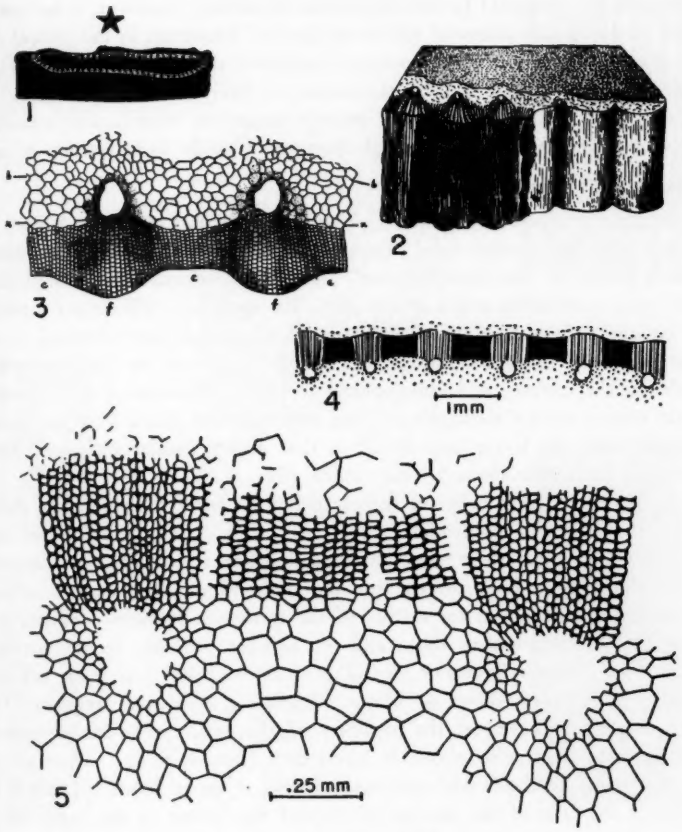
Since that time authors, as Zeiller (1900), Jongmans (1915), Leclercq (1925), Hirmer (1927), Hofmann (1934), Knoell (1935), Emberger (1944), and Arnold (1947) have employed Seward's terminology for calamitean stems with structure preserved. In the meantime, while the term *Arthrodendron* was dangling without a proper description or without having been typified, Ulrich (1910) described some fossil fucoid plants which were found near Kadiak, Alaska, to which he gave the name *Arthrodendron diffusum* gen. et sp. nov.

The term *Arthrodendron* seems more appropriate for a calamite than for an alga of uncertain affinity; also, it has been widely used in the former sense, for it is to be found in all the text-books of paleobotany. Nevertheless, there is no denying the valid priority of *Arthrodendron diffusum* Ulrich (1910), and therefore, I propose the name *Arthroxylon* for calamitean stems of this type.

Because of the historical significance and classical value, as well as the quality and quantity of the preparations of Williamson's specimens, it seemed appropriate that his material be redefined and given a binary name thereby making it the type material for *Arthroxylon*. In order to do so it was necessary to examine the preparations; hence, negotiations were completed with the British Museum of Natural History for the loan of the Williamson Collection of slides of calamites which he called *Calamopitus*. The collection received consisted of 21 preparations in two series, made from two different stems from different localities. In each series there are transverse and longitudinal—both radial and tangential—sections of the stems. Williamson described and figured these two calamitean stems in different articles (Williamson 1871, '71a); the stem of series 52–60 bears the earlier publication date.

A comparison of comparable or homologous sections of the two series, that is, transverse with transverse and tangential with tangential, leaves one with the impression that, although the two stems seem to be essentially similar in type and distribution of cells and tissues, they appear to be fundamentally quite different. As these stems also are patently of different ages, one having more than four times as much secondary wood as the other, the possibilities should be considered: (1) that their differences are more apparent than real because of disparity in age and size; (2) of their being stems of different orders, that is, primary or secondary axes from plants of the same species and consequently of a somewhat different structure; or (3), that the two stems actually are from different species. The first possibility may be rejected because of fundamental differences in cellular structure of the first formed and comparable secondary elements. As to their being stems of different orders—that remains a possibility, for as yet we do not know the range of structural variability of stems of different orders of the calamites so as to be able to say whether one is primary axis and another a lateral branch on the basis of isolated fragments. However, on the basis of primary structure it would seem most expedient, for the present at least, to recognize the two stem fragments as different species of *Arthroxylon*. The stem of series 35–46 is here designated *Arthroxylon Williamsonii*, and the other, series 52–60, *Arthroxylon oldhamium*.



Figs. 1–5. *Arthroxylon Williamsonii*

Fig. 1. Transverse section (about natural size) of a thin-walled *Arthroxylon (Calamopitus)*, imbedded in its dark matrix. Fig. 2. Small portion from opposite the star in fig. 1, viewed diagonally. Fig. 3. Small segment of fig. 1: b, pith cells; x, crenulated outline separating the pith from the persistent woody zone; c, primary medullary rays; f, woody wedges; after Williamson (1871). Fig. 4. Diagram of portion of transverse section of stem (Will. Coll. No. 35). Fig. 5. Detail of portion of transection (Will. Coll. No. 36).

The following brief description of the two species is intended to be supplementary to the original accounts (Williamson 1871, 1871a). While nine of the sections of series 35–46 and six of series 52–60 are longitudinal through nodal regions, yet because of the methods of preparation the orientation of the plane was more or less randomized. For accurate reconstruction of the node, carefully oriented serial cuts are necessary; hence, the sections at hand are inadequate for a detailed description of the nodal region. The nodal region unquestionably is im-

portant and may yet yield further diagnostic characters; moreover, it has not been ignored in the broader phases of this investigation. However, in the present report the internodal region is the only portion considered, since the great bulk of available preparations, or those made in the future, are likely to be of this region. Furthermore, the internodal region does provide diagnostic criteria, and attention is focused on those features which reveal characters thought to be specific in nature.

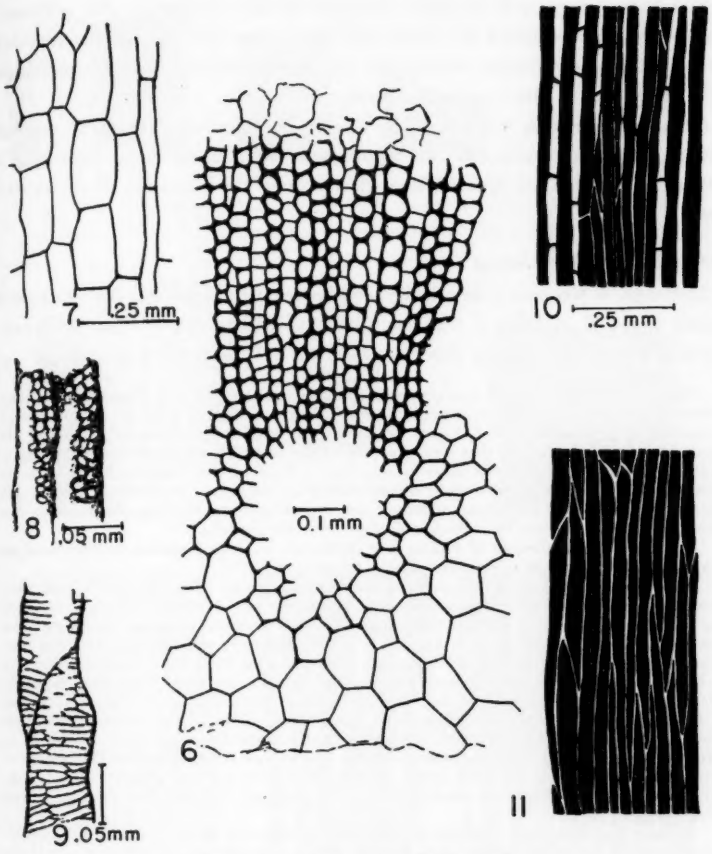
Arthroxylon Williamsonii

This account is based upon twelve preparations (Will. Coll. 35–46) made from a portion of a decorticated stem. Except for the title, "On the Organization of the fossil plants of the Coal-Measures" there is no information in Williamson's article (1871a) as to the origin of this particular specimen. He simply introduced it by saying: "I have next to call attention to a peculiar form identical in many respects with one that I described in the fourth volume of the third series of the Memoirs of the Literary and Philosophical Society of Manchester and to which I gave the generic name *Calamopitus*." The stem measured about 3 cm. in diameter; of this diameter the larger part by far is that of the fistular pith area, for the woody cylinder is only about 0.4 mm. thick (figs. 1, 2).

The thin-walled pith cells are sharply delimited from the secondary elements both in transverse and longitudinal views (figs. 3, 4, 5, 7). The carinal canals, conspicuous because of their relatively large size, appear to have been formed by the disintegration of both protoxylem and metaxylem. The exact number of canals was not determined, for neither of the transverse sections is entire; it was possible to count more than sixty, and the number probably would not exceed seventy. Williamson's figure 19 (fig. 1), which doubtless was made before the material was sectioned, shows 67 canals. Radiating from the canals are 14–17 rows, expanding to 18–20 at the periphery of the woody cylinder, of secondary conducting tissue averaging about 16 layers deep (figs. 4, 5, 6). These are composed of rows of tracheids with interspersed rows of parenchyma. There is some variation in the ratio of the number of rows of the former to the latter but it is usually two to one (figs. 5, 6). The rows of parenchyma—Williamson's "secondary rays"—are not easily distinguishable from the tracheids in transection, but in tangential section they stand out by virtue of their thinner walls and their lesser length (fig. 10).

The markings of the tracheids, which are scalariform to reticulated, are found chiefly, but not altogether, on the radial walls (figs. 8, 9).

The elements of the interfascicular secondary tissue—the "primary medullary ray" of Williamson—are organized in 16–18 radial rows (fig. 5), which are as regularly disposed as are the rows of the fascicular tissue. In transection the dimensions and thickness of the cell walls do not differ greatly from those of the tracheids. These features, that is, disposition, size, and thickness of the walls, combine to make the area appear extraordinarily like the fascicular area. However, upon closer observation some differences become apparent: (1) there is an



Figs. 6–11. *Arthroxylon Williamsonii*

Fig. 6. Detail of woody wedge (Will. Coll. No. 36). Fig. 7. Longitudinal section of portion of pith bordering canal—canal to the right (Will. Coll. No. 44). Fig. 8. Longitudinal radial walls of tracheids of X^2 (Will. Coll. No. 40). Fig. 9. Longitudinal walls of tracheids in vicinity of node (Will. Coll. No. 41). Fig. 10. Longitudinal tangential section of tracheids (shaded) and parenchyma (Will. Coll. No. 37). Fig. 11. Tangential longitudinal section through interfascicular area (Will. Coll. No. 37).

absence of rows of thin-walled parenchyma cells among the rows of thick-walled cells as were found among the rows of tracheids; and (2) in longitudinal section (fig. 11) the thick-walled cells are not only devoid of scalariform and reticulated markings but they are shorter than the tracheids and have a fusiform appearance. In short, these thick-walled fibrous cells appear to have been derived from fusiform

cambial cells and to have matured without further elongation and without the development of specialized secondary thickenings as occurred in the maturation of the tracheids, or without subsequent transverse divisions of fusiform initials as in the formation of the wood parenchyma.

As is shown in figs. 5 and 6, there is some preservation exterior to the woody cylinder. The preservation of this region is so slight as to make description impossible; nevertheless, its presence does clearly show the limitation of the secondary wood.

Arthroxylon oldhamium

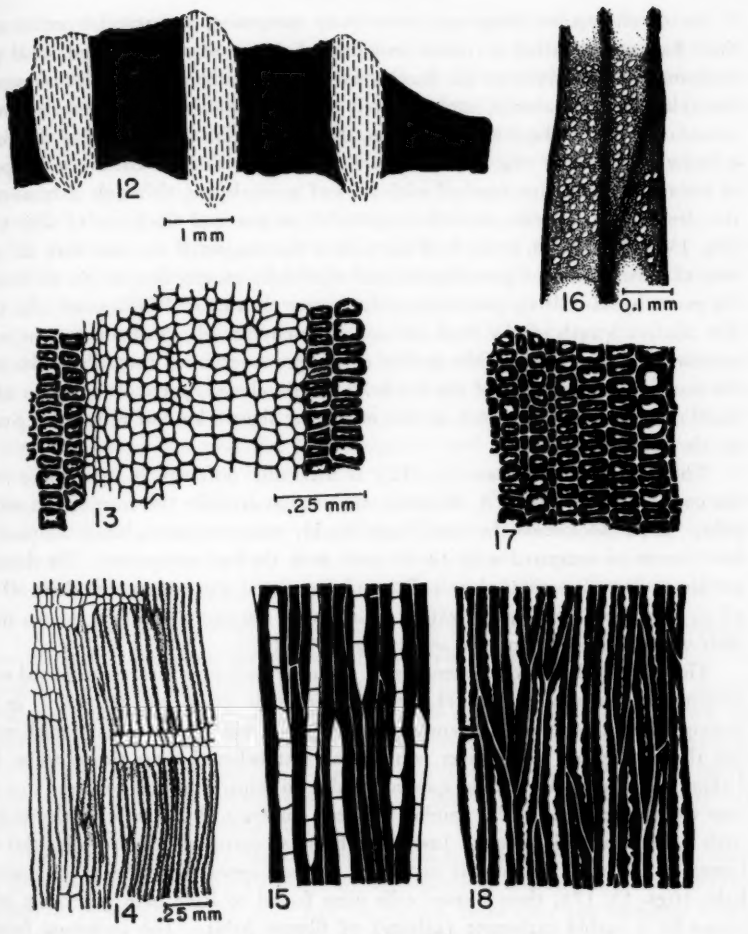
Although Williamson's description of the two specimens of *Arthroxylon oldhamium* appeared in 1871 it was not until much later (1896) that he wrote of their origin and their coming into his possession. His account is as follows:

> Early in the fifties when I was commencing in an unsystematic way to grind down fragments of various objects for microscopic investigations, I found in a drawer of my cabinet a portion of a Calamite that had been extracted from one of the ironstone nodules of the coal measures. I was not at that time provided with a lathe or any other sort of cutting or grinding machinery; but as the calamite presented indications that some structure might be found in it, I chipped off with hammer and chisel such fragments as appeared suitable, and ground them down on a flagstone, obtaining nine curious sections, showing the structure of a woody zone where it was in immediate contact with the medulla.
>
> Having then no intention of making any special use of these preparations, they were put away in a drawer of the cabinet and almost forgotten.
>
> About the same time I had instructed a working joiner to fit up for me a small horizontal grinding wheel, worked by a pedal, and which was not complete. Somehow this little transaction gave the joiner the idea that I was interested in stones; and one evening he called upon me, bringing in his apron a number of rough fragments of sandstone. He had been working at a stone quarry near Oldham, and had picked up from the refuse of the quarry a basketful of stones which appeared new to him, and he concluded that they might be interesting to me. They were in the main the merest rubbish, but amongst them I detected a fragment which was equally elegant and remarkable. How it had escaped destruction from the unprotected way in which it had travelled in such rough company was to me an absolute mystery. The specimen looked like the base of one calamite within the interior of a single joint of another and much larger one; but at that time I was wholly unable to construct any reasonable hypothesis explaining how the two parts had been brought into mutual relationship.
>
> In later days, when the specimen so oddly and accidentally obtained, came to be intelligently studied, its history became clear enough, and the priceless fragment is now one of the most precious gems in my cabinet. Some time after the occurrence of the above event Sir Charles Lyell happened to be at my home, and I showed him this specimen. He was much struck with its interest and novelty, and asked me to allow him to publish a figure of it in the fifth edition of his "Manual of Elementary Geology", upon the preparation of which he was engaged. Of course I consented, and the figure appeared in 1855 on page 368 of that work . . . .[2]

The "nine curious sections" referred to in the above quotation are the sections of Will. Coll. series 52–60. On these slides there are such small pieces of plant material that were it not for Williamson's figures (1871, fig. 2) showing its appearance before being sectioned, its calamitean affinity might be argued.

Preservation of this stem is limited to a very small portion of the secondary woody cylinder. Figure 12, a diagram from the better of the two transverse sec-

[2]The author wishes to express appreciation to Dr. H. N. Andrews for calling attention to the above quotation.



Figs. 12–18. *Arthroxylon oldhamium*

Fig. 12. Diagram of portion of transection of stem (Will. Coll. No. 52). Fig. 13. Detail of portion of fascicular wood bordered on either side by fibrous parenchyma (Will Coll. No. 52). Fig. 14. Longitudinal radial section through fascicular area (Will. Coll. No. 58). Fig. 15. Longitudinal tangential section through fascicular area (Will. Coll. No. 54). Fig. 16. Longitudinal radial walls of tracheids (Will. Coll. No. 58). Fig. 17. Transection of portion of interfascicular area (Will. Coll. No. 52). Fig. 18. Longitudinal tangential section through interfascicular area (Will. Coll. No. 54).

tions, shows the same pattern of rows of fascicular xylem alternating with rows of thick-walled fibrous cells as was found in the former species. It is in the cellular detail and in the proportion of tissues, rather than in tissue pattern, that *A. oldhamium* differs from *A. Williamsonii*.

In *A. oldhamium* there are fewer rows composing a fascicular xylem area; there had not occurred as many anticlinal divisions of tracheid and wood parenchyma initials to increase the number of rows, with the result that in transection the xylem bands maintain approximately the same width from the early formed secondary wood to the peripheral region, that is, in so far as the tissue of the woody cylinder is preserved (fig. 12). As in *A. Williamsonii*, these bands are composed of rows of tracheids interspersed with rows of parenchyma, although in transection the elements of the two are indistinguishable in size and thickness of their walls (fig. 13). But, again, as in *A. Williamsonii*, the tangential sections show the pattern of distribution of parenchyma and tracheids, except that in *A. oldhamium* the parenchyma cells are proportionately shorter than in *A. Williamsonii* (fig. 15). The relative length of the tracheids and parenchyma cells is also shown in radial section (fig. 14). Despite the quality of the preservation of the cells of this stem the markings on the walls of the tracheids remain elusive, particularly in the internodal region; occasional views, as that of fig. 16, show a kind of reticulated pitting on the radial walls.

The interfascicular area (fig. 12) is markedly different in appearance from the corresponding area of *A. Williamsonii*, yet structurally the areas are essentially alike. In *A. oldhamium* the area is considerably more extensive, being composed of 30–35 rows as compared with 16–18 rows as in the former species. The elements are larger in transection, their radial and tangential dimensions are about 42 × 65 μ; they are vertically elongated, their length varying from four to ten times their width, with tapering end walls (figs. 17, 18).

These regularly disposed elements of the interfascicular area are rendered more striking by the simulated thickness of their walls (figs. 13, 17, 18). In his description of this tissue, Williamson wrote: "Each cell appears to have thick walls, like those of recent woody fiber, which I at first believed these tissues to be; but I think that the appearance in question is due to mineral infiltration, and that the true walls were thin." This opinion has been confirmed by examining the sections with a polarizing microscope. Instead of being so extremely thick-walled that the lumen of the cells was almost occluded, as they appear in ordinary transmitted light (figs. 13, 17), these fibrous cells were found to have been selectively infiltrated by a turbid carbonate (calcite) of fibrous habit. The carbonate formed pseudo-spherulite aggregates which show undulose or plumose extinction upon rotation of the object stage of the microscope.[3]

Arthroxylon Williamsonii from an American coal field.—

This stem fragment was found in a coal ball collected by the late Professor A. C. Noé from a strip mine near Petersburg, Indiana. In the Ditney Folio (1902) the coal of this locality is listed as Coal No. 5 of the Upper Carboniferous.

The coal ball was a relatively small one with dimensions of approximately 5 × 6 × 7 centimeters. Like most of these calcareous nodules, it contained an

[3]The author is indebted to Dr. J. C. Haff of the Geology Department of Mount Holyoke College for the polariscopic determination of the mineral content of the cells.

assemblage of diverse plant remains—diverse in the number of genera represented as well as in the organs and tissues. The identifiable plant fragments, in addition to the calamitean stem, were roots and leaves of *Sphenophyllum, Lepidodendron* leaves, *Stigmaria* rootlets, some specimens of *Lepidocarpon,* a bit of tissue from a *Medullosa* petiole, scattered fern sporangia, and some synangia.

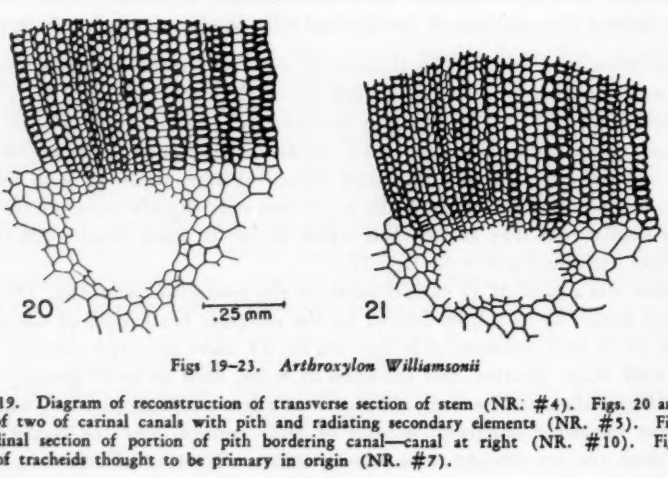
The following description of the specimen of *A. Williamsonii* is based upon 12 thin sections of the coal ball. They are labeled NR 1–12, and are deposited in the Museum of the Illinois State Geological Survey, Urbana, Illinois.

The calamitean material consisted of numerous pieces of wood which, while they were variously disposed and distributed throughout the width of the coal ball, seemed to lie in the same sedimentation plane. Also these pieces are comparable in structure and texture. Therefore, there seems but little doubt of their being parts of a stem that had been crushed and broken and the parts slightly separated before petrifaction. On this assumption all these woody fragments in section No. 5 were projected on paper, then the drawings were cut out and assembled in a ring; this assemblage provided the dimensions and proportions for the reconstruction shown in fig. 19. Preservation of the various tissues of this stem is far from complete, being limited to part of the pith, the elements of the woody cylinder, and occasional remnants of the cambium and phloem of the internodal region; also there seems to have been some chemical alteration of the cell walls which defaced the markings of the lignified cells, leaving the wall surface plain.

The Primary Tissues.—The thin-walled pith cells make a narrow peripheral zone which in transection rarely exceeds four cells deep (figs. 19, 20, 21). In transection the pith cells are roughly isodiametric; the innermost are the largest with an average diameter of about 80 μ, while the outer ones—those bordering the canal and the interfascicular secondary tissue—average about 30 μ in diameter. The cells are vertically elongated, the larger ones only slightly so, while the length of the smaller ones may exceed their width by ten or more times. All the pith cells have horizontal end walls (fig. 22).

There was a total of 42 carinal canals in the assembled pieces (fig. 19). Most of them seemed to have been formed by the complete breakdown of the primary xylem, yet in some instances, as in figs. 20, 21, 24, there are a few elements which, from their shape, position, and thickness of walls, seem to be of primary origin. In one longitudinal section there is a cluster of a few tracheids (fig. 23) which had been cut somewhat obliquely; because of their position near the border of the canal these, too, are thought to be primary xylem. These are the only tracheids in any of the preparations, either longitudinal or transverse, with markings clearly visible; here they are seen as scalariform thickenings on all longitudinal walls.

The carinal canals vary somewhat in shape (figs. 20, 21) but are essentially round in transection with an average diameter of about 350 μ. In comparison with the size of the adjacent pith cells and those of the secondary xylem the canals are larger than in any specimen of calamite I have yet encountered.



Figs 19–23. *Arthroxylon Williamsonii*

Fig. 19. Diagram of reconstruction of transverse section of stem (NR. #4). Figs. 20 and 21. Details of two of carinal canals with pith and radiating secondary elements (NR. #5). Fig. 22. Longitudinal section of portion of pith bordering canal—canal at right (NR. #10). Fig. 23. Cluster of tracheids thought to be primary in origin (NR. #7).

The Secondary Tissues.—In this stem there appears to have been a continuous layer of stelar cambium initiating the secondary tissues, as they form a complete cylinder at the inner margin (figs. 19, 20, 21). Furthermore, the cells are so nearly the same size that under low magnification (32-mm. objective) the transection of the secondary system gives the impression of being a uniform circular band

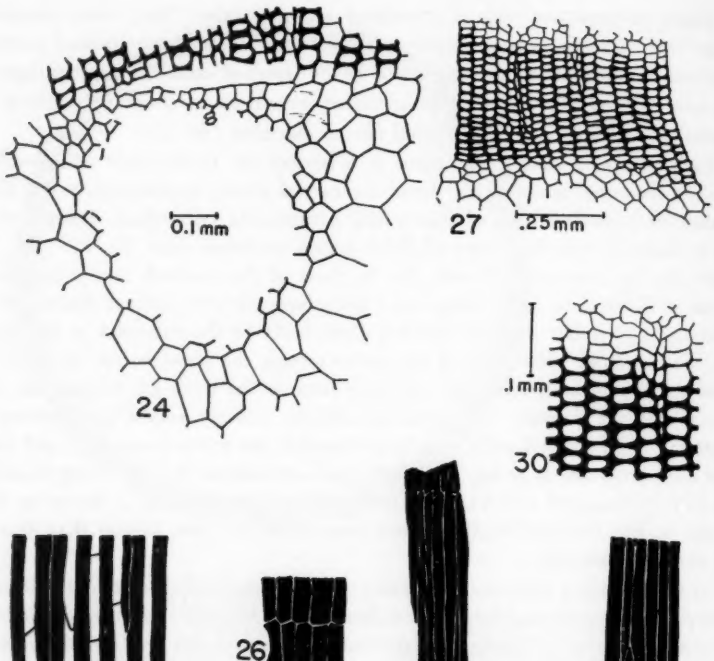
of simple construction with a crenulated outer margin. Yet, when examined under high magnification these tissues resolve into a more complicated pattern. The band of secondary tissues consists of 18–24 layers of cells, the number depending somewhat on the degree of preservation, organized in alternating groups of conducting elements and thick-walled fibrous elements (fig. 19).

Each group of conducting tissue is composed of 14–16 rows of secondary elements radiating centrifugally from the carinal canal; approximately one-third of these are uniseriate rows of thin-walled parenchyma cells which alternate with one to three or even four rows of thick-walled tracheids (figs. 20, 21, 24). In transection the two types of cells, that is, those of the tracheids and parenchyma, are not so different in size or shape, both being squarish with average dimensions of about 25 × 25 μ, but are to be discriminated chiefly by the difference in the thickness of their walls. However, in tangential section the parenchyma, or "rays" as termed by Williamson, stand out not only because the walls are thinner but also because they are shorter. The available sections scarcely exceed a millimeter in length but in all the end walls were to be found in the parenchyma cells, and there were some instances, as in fig. 25, where both extremities of a cell were found in one field. Occasional end walls of tracheids were encountered, as shown in figs. 25 and 26, but tracheid length was not determined as it was greater than that of the sectioned material.

As the secondary elements were being formed there occurred at intervals anticlinal divisions which increased the number of rows to 28–30 at the outer limit of the woody cylinder. Usually the anticlinal divisions were confined to tracheid initials (figs. 20, 21).

Alternating with the conducting tissue (in transection) are bands of fibrous cells of secondary origin arranged in 18–20 radial rows (figs. 19, 27). There are about as many cells in a row as are found in a row of the conducting region, but the radial diameter of the individual cells is less than that of the tracheids, hence the rows are shorter with consequent decrease in the width of this band of tissue as compared with that of the conducting tissue. It is this difference in width of the two types of tissue that is largely responsible for the fluted exterior of the woody cylinder.

Except for the slight difference in shape of the cells composing it this fibrous tissue bears a striking resemblance, in transection, to the conducting tissue; the cells have thick walls, have an average radial diameter of about 22 μ, and a tangential diameter of 37 μ, and were laid down with the same regularity. Yet, as in the former specimen of *A. Williamsonii* and in *A. oldhamium*, closer observation reveals two differences: (1) there is an absence of the thin-walled uniseriate parenchymatous rows; and (2) there had been fewer anticlinal divisions to increase the number of rows, so that this band of tissue remains essentially the same width from its origin at the pith to the peripheral region of the secondary activity (fig. 27). These differences which are noted in transection are verified by longisection.



Figs. 24–30. *Arthroxylon Williamsonii*

Fig. 24. Detail of cells about the carinal canal (NR. No. 5). Fig. 25. Longitudinal tangential section through the fascicular area (NR. No. 6). Fig. 26. Longitudinal radial section through the fascicular area (NR. No. 11). Fig. 27. Transverse section through the interfascicular area (NR. No. 5). Fig. 28. Longitudinal radial section through fibers (NR. No. 6). Fig. 29. Longitudinal tangential section of fibers (NR. No. 9). Fig. 30. Detail of portion of transection of interfascicular area showing cambium (NR. No. 5).

Figures 28 and 29 are longitudinal (radial and tangential) views of these cells; they are vertically elongated, their length being many times their width, with end walls acutely oblique in tangential view. Their walls all appear to be of uniform thickness with no discernible markings. This tissue, therefore, manifests the same homogeneity of its elements and their organization as was found in the comparable area of the two specimens of *Arthroxylon* from the British Coal Measures.

The meager amount of cambium and phloem preserved, of which fig. 30 shows one of the rare instances, would not be worth recording were it not for the fact that it demonstrates the limit of the activity of the stelar cambium.

Some General Considerations and Key.—

In his account of the types of calamitean stems with structure preserved Scott (1920) wrote of *Arthroxylon (Arthrodendron)*: "The *Arthrodendron* type of stem is a rare one. The wood, in the specimens known, is of no great thickness, and the primary bundles are widely separated by primary medullary rays. The chief peculiarity is in the structure of the rays, which are formed, for the most part, of vertically elongated prosenchymatous cells, thus differing widely from the usual parenchymatous structure of these organs." The calamitean stem from an American coal field, described above, shares these generic characters with specimens of *Arthroxylon Williamsonii* and *A. oldhamium* from the British Coal-Measures.

Because of the disparity of geographic origin it seemed possible that the specimen from Indiana would fall into a third species. However, the size and proportion of tissues and the dimension and organization of cells of the material at hand are so markedly like the type of *A. Williamsonii* that the two key down to the same species.

As for *Arthroxylon* being a "rare type"—one can not help wondering whether a reinvestigation of some of the calamitean stems that have been otherwise labeled might not reveal them to be *Arthroxylon*. In transection (many descriptions have been made from transection only) the bands of fibrous parenchyma cells are almost indistinguishable from conducting tissue unless, as in the specimen of *A. oldhamium*, there had been a selective infiltration of mineral which sharply demonstrated a difference of structure of the cells and differentiated and delimited the two tissues. It seems probable, therefore, that in some cases the fibrous tissue in question has been interpreted as interfascicular xylem.

The question might well arise as to why in the present study no use has been made of the character of the wood stressed by Williamson and Scott (1894). According to them, the wood of *Arthroxylon (Calamopitus)* was "characterized by the predominance of reticulated elements in its wood." However, it is my opinion that one might easily overemphasize this character. These specimens do show, as was noted by Williamson and Scott, scalariform pitting of the primary wood (fig. 23), scalariform to reticulated pitting in the tracheids of the nodal region (fig. 9), and reticulated pitting in the secondary wood (figs. 8, 16). Yet the type of reticulation (pit) may well depend on the differential amount of erosion of the border prior to preservation. Therefore, until more is known of the type of reticulation, that is, of the pit types in calamitean secondary wood, it has been thought best not to stress this feature in the present key and diagnosis.

KEY TO GENERA OF CALAMITE STEMS WITH STRUCTURE PRESERVED, AND TO SPECIES OF *ARTHROXYLON**

1. Secondary interfascicular area composed of parenchyma and tracheids.... *Arthropitys*
1. Secondary interfascicular area composed of parenchyma only.
   2. Interfascicular parenchyma composed of alternating radial bands of thick- and thin-walled cells..... *Calamodendron*
   2. Interfascicular parenchyma composed of essentially similar cells..... *Arthroxylon*
      a. Interfascicular area of 16–18 rows; radial and tangential diameter of elements 26 × 34 μ..... *A. Williamsonii*
      a. Interfascicular area of 30–35 rows; radial and tangential diameter of elements 42 × 65 μ..... *A. oldhamium*

* Based on transection of the internodal region.

Arthroxylon Reed, nom. nov.[4]

Calamopitus Williamson, Mem. Manchester Lit. and Phil. Soc. III, 4:174, figs. 1–17. 1871. (Without type; no species indicated or described).

Calamopitys Seward, Fossil Plants 1:301. 1898. (Without species). Not *Calamopitys* Unger, Denkschr. K. Akad. d. Wiss. Wien. 1:159. 1856.

Arthrodendron Scott, in Seward, Fossil Plants 1:301. 1898. (As subgenus; without type; no species indicated or described). Not *Arthrodendron* Ulrich, Harriman Alaska Series (Smithson. Inst.) 4:138, pl. XIV, figs. 1–3. 1910.

Calamitean stem with internodal region of stele organized in alternating bands (as viewed in transection) of conducting tissue and fibrous parenchyma. Bands of parenchyma as wide or wider than the bands of conducting tissue, composed of fusiform cells with walls as thick as those of the tracheids.

Arthroxylon Williamsonii Reed, sp. nov.

Stems with about 70 large carinal canals (diameter up to 360 μ). Secondary conducting tissue composed of 14–17 rows of tracheids with interspersed rows of parenchyma radiating centrifugally from the carinal canal; the number of rows gradually increased by anticlinal divisions of tracheid initials. Both tracheids and parenchyma roughly squarish in transection with an average dimension of about 22 μ. Bands of fusiform parenchyma cells organized in 18–20 radiating rows, cells with an average radial diameter of 26 μ and tangential diameter of 34 μ.

Horizon: British Coal-Measures; American Upper Carboniferous.

Material: Twelve thin sections (Williamson Collection 35–46) in Geology Department of the British Museum of Natural History; 12 sections (NR 1–12) in the Museum of the Illinois State Geological Survey, Urbana, Illinois.

Type: Williamson Collection No. 35.

Arthroxylon oldhamium Reed, sp. nov.

Secondary conducting tissue composed of 8–10 rows of tracheids with interspersed rows of parenchyma. Very few anticlinal divisions, with the result that the bands of tissue remain virtually the same width from the inner limit at the carinal canal to the peripheral region. Tracheids and parenchyma cells roughly squarish in transection with average dimensions of 44 μ. Bands of fusiform

[4] The generic name is derived from Αρθρον—articulated, and Ξυλον—wood.

parenchyma organized in 30–36 radial rows; cells with average radial diameter of 42 μ and tangential diameter of 65 μ.

Locality and horizon: Sandstone-Quarry near Oldham, British Coal-Measures.

Material: Nine sections (Williamson Collection Nos. 52–60) in the British Museum of Natural History, London.

Type: Williamson Collection No. 52.

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SOME AMERICAN PETRIFIED CALAMITEAN STEMS

HENRY N. ANDREWS*

Descriptions of structurally preserved stems referable to the Calamitaceae (as treated by Hirmer, 1927) are notably few in the American literature. A fragmentary calamitean stem was reported by Reed in 1926, and the same author later (1938) described a young stem under the name *Calamites multifolia.* Several other authors have recorded the occurrence of petrified calamitean stems in American coal balls (see Andrews, 1951), but no comprehensive or critical accounts have been given previously.

Up until a few years ago the numerous coal balls which had been cut in my laboratory revealed almost no fossils of this group. This was rather puzzling in view of the fact that pith casts and foliage referable to the Calamitaceae are not rare in the American coal fields. Apparently, our earlier collections had been made from spots where calamitean stems did not chance to have been deposited, for during the past four years we have accumulated stems and roots in some abundance.

The specimens described here came from several localities in Illinois, Iowa, Indiana, and Kansas, and represent the three genera *Arthropitys, Arthroxylon* and *Calamodendron.* Certain of the species are closely comparable with European ones while others show quite distinctive characters. Several specimens have come from the Calhoun horizon in the upper part of the McLeansboro group in southern Illinois; some are from the Petersburg No. 5 coal north of Booneville, Indiana; several coal balls containing well-preserved stems and roots have been turned over to me by Dr. A. H. Blickle who collected them near Oskaloosa, Iowa. However, by far the most prolific source has been the vast coal-ball supply in the Fleming coal which is mined near West Mineral, Kansas. At this last locality it is evident that the calamites composed a significant element of the Carboniferous vegetation. More precise data concerning the horizons at which these plants were found will be given under the species descriptions, and for additional information the following references may be consulted: Abernathy, 1946; Andrews, 1951; Schopf, 1941; Andrews and Mamay (1952).

Although the generic name *Calamites* was originally assigned to pith casts where the cellular structure was unknown it has been generally applied in a rather loose manner to both stems and plants as a whole. In the following pages I will use the term "calamitean" to refer to stem remains of plants referable to the Calamitaceae as defined by Hirmer (1927, p. 381).

In many cases it is rather easy to recognize calamitean stems in a freshly cut coal ball or where they are exposed on a weathered surface prior to any treatment. The lack of much pith tissue, presence of protoxylary canals, and characteristic banded appearance of the secondary wood are distinctive characters. It is quite another matter to identify the fossils specifically, and as Miss Reed has pointed out

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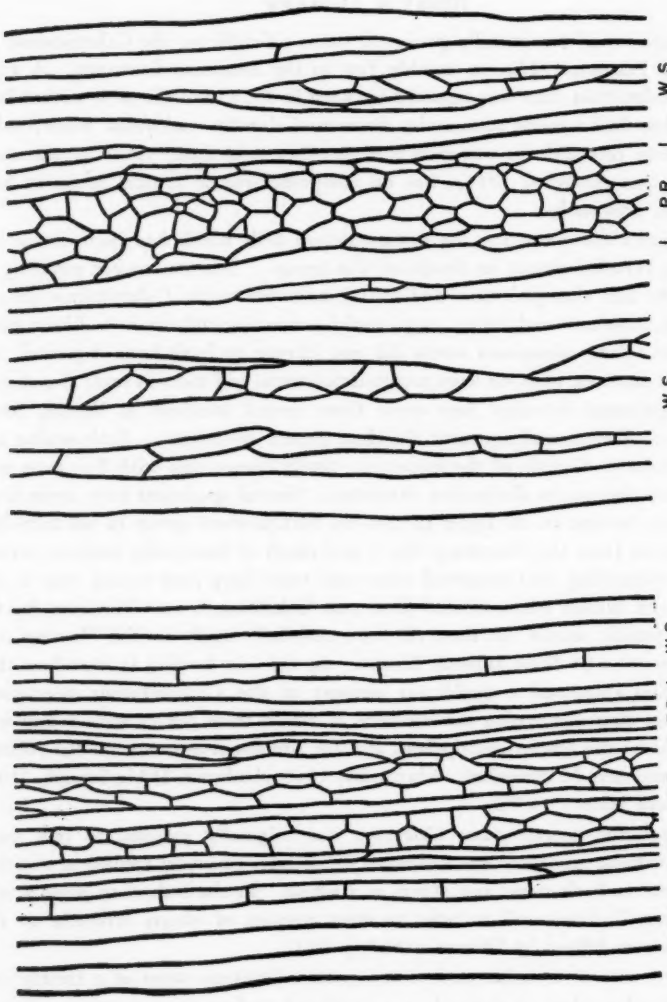
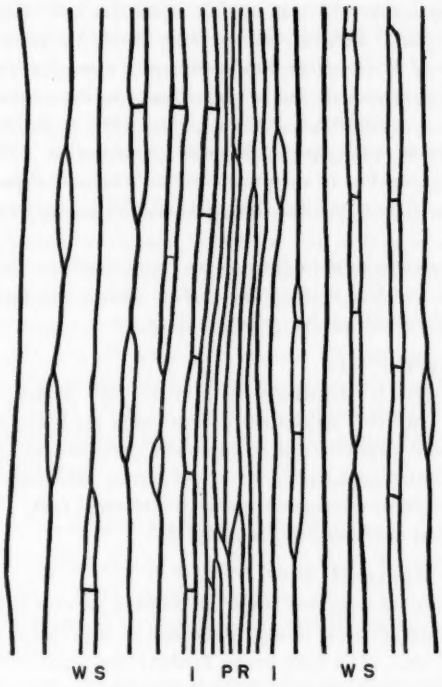


Text-fig. 2. *Arthropitys kansana*

Text-fig. 1. *Calamodendron americanum*

Text-figs. 1–3. Tangential sections of *Calamodendron*, *Arthropitys*, and *Arthroxylon* respectively, showing the comparative anatomy of the wood; all are camera-lucida drawings × 35: WS, wood sector; FB, fiber band; PR, primary ray.



Text-fig. 3. *Arthroxylon Williamsonii.*

in the preceding contribution, tangential sections are necessary for positive generic identification. In order to discuss this problem I shall devote more space than is ordinarily necessary to brief reviews of the history and taxonomic status of the genera concerned. Much of the pertinent literature is not readily available, and since it is evident that our work to date is only introductory to the American fossils of this group it is hoped that the supplementary information presented here may be of aid in future studies. A considerable number of genera of articulate cones are now known from American coal balls, some of them of excellent preservation and distinctive organization, yet much remains to be accomplished in classifying the stem remains and correlating them with the cones.

The petrified calamitean stems are known chiefly from the works of Williamson, Scott, Renault, and the more recent contribution by Knoell. Williamson and Scott, in their several papers on these fossils, have given us an excellent general understanding of the curious stem anatomy, but taxonomic considerations appear to have been of less concern to these English workers. Little attention was given to specific entities of *Calamites* (stems now assigned to *Arthropitys*), and in the unique *Arthroxylon*, a fossil described and illustrated in excellent fashion by

Williamson as long ago as 1871, no specific name has been assigned prior to Miss Reed's present account. Renault, on the other hand, has recorded a considerable number of species of *Arthropitys* and several of *Calamodendron*. While certain of these are based on specimens that are insufficient in size or preservation to allow the establishment of a significant binomial, they serve to convey a knowledge of character variation in the group. Knoell's contribution (1935) adds to our knowledge of the group but in the present writer's opinion depends too heavily on transverse sections. The reason for this criticism will be apparent in the following pages.

The petrified calamitean stem remains are segregated into three genera: *Arthropitys*, *Arthroxylon* and *Calamodendron*. Before considering each in detail it may be useful to record the distinctive generic characters.

ARTHROPITYS Goeppert, 1864

The wood sectors[1] are separated by primary rays which vary from one to several cells wide. In many species the primary rays are broad conspicuous bands, and they may extend undiminished to the outer periphery of the xylem or taper abruptly. In the latter instance the outer portion of the secondary wood consists of a more or less uniform mixture of tracheids and small rays. The ray cells in all cases are more or less brick-shaped (text-fig. 2).

CALAMODENDRON Brongniart, 1849

The wood sectors are separated from the primary rays on either side by fibrous bands, the radial sequence thus being: wood sector, fiber band, primary ray, fiber band, wood sector, etc. The fiber bands flanking the wood sector may equal the latter in (tangential) thickness or be considerably less (text-fig. 1).

ARTHROXYLON Reed, 1952

The wood sector appears essentially similar to that of the two genera cited above. The primary rays, however, consist of vertically elongated cells several times as long as broad and present a striking contrast with *Arthropitys* or *Calamodendron* or in fact with the "rays" of any other stem exhibiting secondary wood (text-fig. 3).

In so far as these three genera are known the significant features lie in the secondary xylem. Several authors have described specimens of small twigs in which little or no secondary growth is present, and in some cases specific names have been applied to such remains. While future studies may reveal ways of identifying more precisely such remains, a comparison with any of the above-cited genera usually appears to be arbitrary. One must have a way to handle such specimens, and Reed's (1938) solution of assigning them to *Calamites* seems satisfactory. There is no reason to doubt that the three genera, *Arthroxylon*, *Calamo-*

[1] The secondary xylem of most calamitean stems is composed of two distinct tissue systems: the *wood sectors* which radiate from the protoxylary canals and consist of tracheids and small rays; and alternating *primary rays* which are in direct contact with the pith and are parenchymatous in nature. The term *secondary ray* is used here to refer to the (usually uniseriate) rays which occur interspersed among the tracheids in the *wood sector*.

dendron, and *Arthropitys*, so distinct in the organization of their secondary wood, are all responsible for the common pith casts assigned to *Calamites*. The latter is thus a more "inclusive" genus and perhaps suitable for small petrified stems.

In only a few instances have stems been reported in which the cortical tissues are preserved. One such specimen described as a "Calamite stem" by Seward (1898, fig. 78) indicates that a considerable abundance of cork tissue was present in the larger branches.

A point that is deserving of special note here is the problem of distinguishing the three genera in transverse section. It may be that with especially well-preserved specimens and much experience on the part of the investigator this is possible, but the rather close similarity of the several cell types involved renders it otherwise difficult. In *Calamodendron*, with its fibrous bands between the wood sector and primary ray, the transverse section may reveal the specimen's generic affinity but with the other two the problem is more acute. In the case of the *Arthroxylon* reported below I assumed from the transverse section that it was a species of *Arthropitys*, and it was only when the tangential section was studied that the distinction became evident.

Arthropitys Goeppert

There have been some eighteen or more species and varieties assigned to this genus although several of them are based on fragmentary and incomplete material. Most of the descriptions are to be found in the contributions of Renault, Goeppert, and Knoell, cited below.

A considerable degree of variation is present in the organization of the primary ray. It may retain a considerable breadth throughout the secondary xylem; it may taper off quite abruptly; or be lacking from the start, although in a single specimen the organization is generally quite constant. When the primary ray tapers rapidly the anatomy presented by a tangential section must be carefully correlated with the transverse view. For example, figs. 6 and 7 illustrate the difference that may be encountered in a single specimen. Care must also attend the use of the transverse section with reference to its proximity to the node.

Other characters have been used such as the size of the stem, extent of secondary growth, length of internode, nature of the tracheidal pitting, and the size of the protoxylary canals. Of these characters, the first two are obviously a reflection of ontogenetic development and require no further comment. The length of the internode may be significant if the specimens are long and abundant and thus subject to statistical analysis, but it seems of doubtful value with a small isolated specimen. With reference to the pitting, both scalariform and the round, crowded bordered pits are found in the genus. In any individual specimen one type is usually predominant although transitions are not uncommon. The size of the protoxylary canals varies considerably, and this may be of use as a supplementary character. Renault has reported one specimen *(A. gigas)* in which they are

lacking. In this connection I would like to note that certain of the specimens of *Arthropitys* that I have examined appear to display tracheids internal to the protoxylary canal. A more detailed discussion of this will be found under the description of *Arthropitys* sp. A.

This account is by no means intended as a monographic treatment of the genus. It seems useful, however, to cite briefly below the supposedly distinct features of certain species as a matter of recording structural variation in the genus and for the purpose of comparison with the American fossils.

ARTHROPITYS BISTRIATA (Cotta) Goeppert, 1864

As figured by Renault, 1895 (see especially pl. 4, fig. 3; pl. 5, figs. 8, 9), the secondary wood is composed of uniform wood sectors and primary rays, the latter being 6–7 cells wide (nearly as broad as the wood) and extending vertically from one node to the next. Small rays are present in the wood sectors. The pitting of the tracheids appears, in Renault's figures, to be predominantly scalariform with a tendency toward reticulate-bordered arrangement. This species is based on Cotta's *Calamitea bistriata* described in 'Die Dendrolithen', and I believe should be accepted as the type species. Goeppert's figures do not display all of the distinctive characters as well as might be desired. For example, his fig. 1 on pl. 33, a transverse view of a portion of the stele, does not show the protoxylary canals. Renault's description (1895) is very thoroughly illustrated. Origin: Permian, Chemnitz, Germany.

ARTHROPITYS COMMUNIS (Binney) Hirmer & Knoell (in Knoell, 1935)

This species was originally described by Binney (1868) as *Calamodendron commune*. It is discussed by Williamson and Scott, 1895, and in Williamson's earlier contributions. While presenting splendid anatomical studies Williamson and Scott were not concerned with the assignment of specific names. The most recent treatment is that of Hirmer and Knoell (in Knoell, 1935) where the plant is formally assigned to *Arthropitys*. This is a species which attained considerable size; it possesses scalariform pitted tracheids and large primary rays which usually taper rather abruptly.

ARTHROPITYS EZONATA Goeppert, 1864

This species is based on a rather small fragment. The primary rays appear narrow, little larger than the rays in the wood sector; the pitting is scalariform. Origin: Permian; Chemnitz, Germany.

ARTHROPITYS GALLICA Renault, 1896

This is represented by a large stem reported to be 24 cm. in diameter (apparently this refers to wood only). Numerous resin cells are present in the peripheral pith zone, and the tracheids display scalariform pitting. The primary rays are initially broad but do not remain so throughout the wood as in *A. bistriata*. It is reported to differ from *A. approximata* (see below) by its over-all size and length of internodes, characters which seem to be of doubtful significance. Origin: uppermost Carboniferous; Montrambert, near Saint Etienne, France.

ARTHROPITYS APPROXIMATA (Schlotheim) Renault, 1896

According to Renault, "Cette espèce se distingue facilement de l'*Arthropitus bistriata* par sa taille plus petite, par ses entre-noeuds qui sont plus courts, par ses verticilles ramifères qui sont plus fréquents" (1896, p. 310). It is my feeling that these characters, while they may distinguish a *specimen*, actually are of little specific value. Origin: Upper Carboniferous; Saint Etienne, Commentry, Autun, in France.

ARTHROPITYS LINEATA Renault, 1876

Large primary rays are initiated in this species but almost immediately disappear, so that the secondary xylem for the most part consists of tracheids rather regularly interspersed with small rays. The tracheids are scalariform.

ARTHROPITYS MEDULLATA Renault, 1896

This species is apparently very similar to *A. lineata* in the general organization of the secondary wood. It is reported to have a small pith (cavity) and relatively abundant wood. Origin: Upper Carboniferous; Autun, France.

ARTHROPITYS GIGAS (Brongniart) Renault, 1896

This is a large species described as attaining a diameter of 50 cm. The tracheids bear numerous rows of round pits, and protoxylem canals are reported to be lacking. Origin: Permian; Autun, France; the "grès rouge inférieur de Saarbruck; and the grès cuivreux de Nidji-Troisk, district de Bjelebey, de Piskork, Orenbourg, Russia."

ARTHROPITYS ROCHEI Renault, 1896

This is also represented by large specimens. It is distinguished from *A. gigas* by the presence of protoxylary canals as well as more numerous and larger secondary rays in the wood sectors. The tracheids display numerous bordered pits. Origin: Upper Carboniferous and Permian; Champ des Borgis, France.

ARTHROPITYS BISTRIATOIDES Hirmer & Knoell (in Knoell, 1935).

The secondary wood is present but not strongly developed; the primary rays and wood sectors appear to maintain equal tangential dimensions. Origin: Westphalian A; "Floz Katharina des Ruhrgebiets."

ARTHROPITYS HIRMERI Knoell, 1935

The secondary wood is strongly developed and homogeneous, no large primary rays being present. Origin: Westphalian A; "Floz Katharina des Ruhrgebiets."

ARTHROPITYS JONGMANSI Hirmer (in Knoell, 1935)

Very little secondary growth is present; the protoxylary canals are very large and the primary bundles numerous; abundant thick-walled parenchyma cells form conspicuous arcs on the inner side of the canals. Origin: Westphalian A; "Floz Katharina des Ruhrgebiets."

ARTHROPITYS HERBACEAE Hirmer & Knoell (in Knoell, 1935)

The central (pith) canal is large, and almost no secondary wood is present. There are certainly no distinctive characters here, and the authors admit that it may be only a young condition of some other species.

In spite of the difficulty of defining clear-cut species of *Arthropitys* it is evident that there is considerable variation. Aside from the difference in pitting the most striking feature is the variation in wood sector-primary ray relationship, and it seems possible to the present writer that this may serve as a reasonable basis for further generic segregation.

ARTHROPITYS COMMUNIS (Binney) Hirmer & Knoell, var. **septata** Andrews, var. nov.

The following description is based on specimens No. 722 and 804 found in coal balls from the Calhoun horizon near Berryville, Illinois.

The most complete specimen (figs. 1, 2) consists of a stem fragment about 18 cm. long and a maximum diameter of the secondary wood of nearly 7 cm. The phloem and cortical tissues are not preserved. If, however, abundant periderm was developed, as described by Seward (1898, figs. 78, 79) for certain English specimens of *Arthropitys*, this one from Berryville represents a trunk of 6–8 inches in diameter.

The stem presents a striking appearance by virtue of seemingly large, more or less oblong "canals" in the periphery of the pith. These are well shown in fig. 1. Although the "canals" probably represent decay areas and consequently are of no taxonomic significance, their regular arrangement suggests some sort of cellular differentiation. Another specimen has been observed which shows a tendency of the pith cells to disintegrate at rather regular intervals around the periphery. This decay, if carried further, would produce the effect shown in fig. 1.

Certain of the pith cells in the peripheral region are larger than the others and display dark contents which suggest a secretory nature. However, in all, it is not easy to distinguish these apparent secretory products from iron sulphide. Renault has reported resinous cells in the pith of *A. gallica*.

Outside of the pith the preserved part of the stem consists of a strongly developed zone of xylem which attains a (radial) width of about 15 mm. This consists of scalariform tracheids and parenchymatous rays. Before considering the secondary tissues in detail we may note first the protoxylary canals which are very small and at many points appear to be lacking. Slight differences in the quality of preservation make it difficult to appraise these at all points but in places where the preservation is excellent no canal can be observed and at others only small ones are to be noted (fig. 10). Renault (1896) reported protoxylary canals lacking in *A. gigas*.

Figure 2, a representative sector of the secondary xylem, shows radially elongate wedges of tracheids (wood sectors) separated by broad parenchymatous primary rays. Going radially from pith to periphery of the wood it will be noted that the

rays gradually decrease in their tangential dimensions or rather lose their distinctive appearance by the admixture of rows of tracheids.

The tracheids are uniformly scalariform (fig. 8), and their morphology presents a point of some interest. When first studying tangential sections taken only a few cells from the protoxylary canal I observed what appeared to be a considerable admixture of rays, a rather surprising point since such rays were not evident in the transverse view. Further observation with both radial and tangential sections revealed that the tracheids are profusely septate (fig. 5) near the inner limits of the secondary wood, the septations being for the most part horizontal walls. The tracheids average about 44 μ in diameter, and the length of the inner secondary tracheids may likewise be no more than 44 μ. That is an extreme case but cells 100 μ long are not uncommon although lengths are very variable. At a distance of 2 mm. farther out, the tracheids are many times longer than wide; in fact, it is nearly impossible to follow cells through their entire length due to the interference of rays, but the septations are still evident. Scott (1920, p. 25) mentions the occurrence of transverse walls in the tracheids but indicated that they are not frequent; his discussion of calamitean anatomy is rather general but he is presumably referring to *Arthropitys communis*. In this specimen from Illinois the septations are very abundant and it was not until several mm. of secondary wood were formed that the tracheids assumed great length and predominantly tapered ends.

The primary rays (figs. 1 and 10) are initiated as broad parenchymatous bands of .5 mm. or more in width and extend vertically from one node to the next. In passing out radially through the wood two changes are notable; the tangential dimensions of the primary rays gradually decrease until, at a distance of 6–7 mm. from the pith, they are no longer readily distinguishable. This statement is of course subject to a certain amount of variation; the second change is in the decrease in size of the cells composing the rays.

As might be surmised, the tangential sections present corresponding differences depending on their position from the pith. Figures 6 and 7, shown at the same magnification, display the tangential aspect at points .5 and 11 mm. respectively from the pith.

The more striking features of these sections may be noted briefly:

Figure 6.—The primary ray cells, although very variable in size, range up to 120 μ in width (tangential). The structure of the wood sector is not easy to interpret due to the presence of a considerable number of septate tracheids, but it appears that secondary rays have already been initiated.

Figure 7.—The ray cells are generally smaller, not often exceeding 70 μ in tangential dimensions. The tracheids are greatly elongated and are interspersed with abundant secondary rays which are 1- to 3-seriate and of very variable height. When observed in radial view the ray cells appear (fig. 9) quite uniform in size, averaging about 44 μ wide and 108 μ high.

A comparison of this Illinois *Arthropitys* with the better-known species described by Renault and by Knoell seems to indicate that the closest relationship lies with *A. communis*. The comparison is close although there are certain differences which seem to justify at least varietal distinction. These differences are principally: (1) the small size of the protoxylary canals; (2) the abundant septation of the tracheids in the earlier formed secondary xylem; (3) the lack of pronounced tangential elongation of certain of the cells of the primary rays (cf. Knoell, 1935, pl. 2, fig. 6A).

Diagnosis:

Primary rays diminishing in tangential dimensions rather rapidly; protoxylary canals small and sometimes lacking; inner tracheids profusely septate; secretory cells present in pith.

Horizon and age: Calhoun coal, upper McLeansboro group; Upper Pennsylvanian.

Locality: Brian farm, near Berryville, Illinois.

Type specimen: Coal ball No. 722, Henry Shaw School of Botany, Washington University, St. Louis.

A Small Calamitean Stem from Berryville, Illinois.—

A few very young calamitean stem specimens may be recorded briefly although their development is not sufficiently advanced to allow generic designation.

Two small stems, one of which is shown in fig. 4, have been found which measure about 1.3 mm. in diameter. They consist of only a few layers of pith cells, about a dozen protoxylary canals, and a broad cortex. A few tracheids may be noted around the outer periphery of each canal, resembling in this early stage the structure in the modern *Equisetum*. The phloem cannot be observed, a break between the xylem and inner cortex apparently representing the cavity left by the decay of that tissue. Numerous cells in the inner part of the cortex are distinguished by having either dark, thick walls or a dark (resinous?) substance in the periphery of the cell lumen.

In the same coal ball (No. 756) which contained these minute stems a somewhat larger stem appears with secondary growth evident. The same dark substance may be noted in some of the inner cortical cells as indicated above, and there seems to be little doubt that this is a somewhat older stage. Although there is not a great deal of secondary xylem developed in this specimen (fig. 13), it seems very possible that it belongs to *Arthropitys* and by virtue of the similarity of the cortex one may infer that the smaller stems (fig. 4) do likewise.

Calamitean Stems from Kansas.—

Numerous calamitean stem specimens have been obtained from the strip pit of the Pittsburg and Midland Coal Mining Corporation located about four miles south of the town of West Mineral, Kansas. This horizon is the Fleming coal which occurs in the upper part of the Cherokee shale and is approximately of mid-Pennsylvanian age. Coal balls are found here in an unparalleled abundance (see

Andrews and Mamay, 1952), hundreds of tons of them being used for road-building material. A considerable portion of them are heavily pyritized although specimens of excellent quality are not rare.

By comparison with any other American coal ball locality with which I am familiar, or with any reported in the literature, the calamitean stems are notably abundant. We have encountered some scores of specimens, although many of the strongly pyritized ones have been discarded in the field; from the abundant specimens several distinct species have been recognized.

ARTHROPITYS **kansana** Andrews, sp. nov.

This description is based on specimen Nos. 755 and 786. No. 755, which is designated as the type, is a nearly complete transverse section of a stem (fig. 14) in which the xylem attains a thickness of 14 mm. No. 786 is a fragmentary sector of a larger stem in which the xylem attains a thickness of about 23 mm. and probably represents a stem of 8–10 inches in diameter. Both specimens are partially pyritized, although No. 786 is notable in that certain portions of the wood are quite lacking pyrite and are exceptionally well preserved. There is an appreciable thickness of pith tissue present, and the protoxylary canals are rather large, averaging about 200 μ in diameter.

The most distinctive feature of the wood lies in the uniform width of primary rays and wood sectors throughout the extent of the xylem (fig. 14). There is to be sure some variation in organization of the primary rays. They tend to lose their identity by the admixture of tracheids in their outer course but for the most part they continue more or less undivided, and the contrast with the *communis* type (fig. 2) is rather striking. As viewed in tangential section (fig. 11), the primary rays may be noted to extend vertically from one node to the next, and aside from the occasional interruption by a tracheid they are quite uniform in their tangential dimensions. The wood sectors consist of tracheids (fig. 12) interspersed with secondary rays (figs. 11, 17, 26) of very variable dimensions. The latter may be uniseriate and only 2–3 cells high, and at the other extreme rays 3–4 cells wide and many cells tall are present.

This *Arthropitys* from Kansas seems to compare most closely with Renault's species *A. rochei* and *A. porosa*. The tracheid-ray relationship, however, does not seem to be sufficiently close to admit inclusion in either of these species a certainty. Renault's illustrations of *A. rochei* are not adequate to allow accurate comparison. *A. porosa* is based on a small fragment but judging from Renault's (1896) fig. 7, pl. 7, the Kansas fossil differs most notably in the abundance of secondary rays.

Diagnosis:

Stem with strongly developed secondary wood; protoxylary canals relatively large; primary rays narrow but uniform throughout the radial extent of the wood; woody sectors interspersed with numerous secondary rays which vary much in size; radial walls of tracheids with circular to slightly elongate bordered pits.

Horizon and age: Fleming coal, upper part of Cherokee shale, Missouri series; mid Pennsylvanian.

Locality: from strip mine located four miles south of West Mineral, Kansas.

Type specimen: coal ball No. 755, Henry Shaw School of Botany, Washington University, St. Louis.

ARTHROPITYS sp. A

Our Kansas collections include a specimen (No. 805) which is interesting in several respects but because of imperfect preservation I hesitate to assign a specific name to it. It consists of a fragment of a stem the woody cylinder of which must have exceeded 6 inches in diameter, thus representing a stem perhaps a foot or more thick in life. Some concept of its size may be gained from the fact that the wood attains a thickness of 5 cm. Unfortunately, the pith tissue is entirely decayed and the wood is rather badly shattered.

When viewed in transverse section the protoxylary canals (figs. 16, 23, 24) appear to be surrounded by a distinctive band of thick-walled cells which seem to represent an appreciable development of centripetal wood. Series of longitudinal peels were prepared through several of the canals in an attempt to determine the nature of the pitting of these cells. Although they are thick-walled and of great length, quite in contrast to the pith cells, I have been unable to observe any specialized thickening of the wall to confirm the supposition that they represent centripetal wood. The first 3–4 centrifugal cells also lack pitting, evidently through lack of preservation, so that I believe there is no reason to doubt that the inner cells represent centripetal tracheids. Aside from these small cells immediately surrounding the protoxylary canal, the tracheids show predominantly very elongate bordered pits. Occasionally, however, circular bordered pits may be observed.

ARTHROPITYS sp. B

This (No. 753) is another rather large stem the woody cylinder of which must have been about 5 inches in diameter in life. It is quite similar to that of *A. kansana* except that the tracheidal pitting is predominantly scalariform (fig. 21). Certain areas, however, show a tendency toward the reticulate-bordered type (fig. 22). From my own observations and judging from previously described species the nature of the tracheidal pitting in the secondary wood of the calamitean stems is quite constant, being either scalariform or of the reticulate-bordered type.[2] In view of the variation displayed in this specimen, however, I am reluctant to assign it a distinct specific name. It is of interest from the standpoint of variation in characters displayed by these several Kansas specimens, but it seems desirable to await further information before making a binomial committment.

[2]It may be noted, however, that Renault shows a remarkable combination of multiseriate bordered circular to elongate pitting (nearly scalariform) in *Calamodendron intermedium* (Renault, 1898, pl. 2, fig. 3). His figures indicate that a particular cell is clearly of one pattern or the other, which lends a rather striking appearance.

Calamodendron Brongniart

The genus *Calamodendron*, characterized chiefly by the fibrous cells which occupy a position between the wood sector and primary ray, is represented in the author's collection by one specimen from the Mineral, Kansas, locality.

Three species have been described by Renault which may be briefly characterized:

Calamodendron striatum Brongniart (see Renault, 1898, p. 381).

Relatively narrow fibrous bands are found on either side of the woody sector and the primary rays are narrow. Renault's fig. 4, pl. 1, shows the fibrous band as consisting of about 6–8 cells and indicates uniformity throughout the xylem. The tracheids bear elongate pits. Origin: Permian (Rotliegendes); Champ des Borgis and Margenne, France.

Calamodendron congenium Grand 'Eury (see Renault, 1898, p. 386).

The wood sectors are narrower than the flanking fibrous (prosenchymatous) bands, thus presenting a relationship inverse to that found in *C. striatum*. The tracheids display multiseriate bordered pits. Origin: Upper Carboniferous; Saint Etienne, France.

Calamodendron intermedium Renault (1898, p. 371).

The general relationship of the primary rays, fiber bands, and wood sectors is similar to that of *C. congenium*. The tracheids have elongate bordered pits as in *C. striatum* or multiseriate bordered pits as in *C. congenium*, whence the specific name. Origin: Upper Rotliegendes; Autun (Champ de Borgis), France.

Calamodendron **americanum** Andrews, sp. nov.

This species is represented in our collections from Kansas by one specimen (No. 709) 27 cm. long with a woody cylinder 26 mm. in diameter. The pith area, although not preserved, is small, measuring about 3.5 mm. in diameter, and the wood attains a radial thickness of about 11 mm.

In view of the lack of pith, of protoxylary canals, and extra stelar tissues, the description is necessarily based on the secondary xylem (fig. 29). When viewed in tangential section, the primary rays are seen to be flanked on either side by 3–5 fibrous cells, and the ray proper is occasionally interspersed with the fibrous cells. The latter are, for the most part, readily distinguishable from the tracheids, being thicker-walled and averaging about 16 μ in diameter while the tracheids are about twice that size.

The smaller secondary rays may be observed scattered among the wood sectors although the heavy pyritization of that part of the wood renders study difficult. The tracheids are of the multiseriate bordered type.

When compared with the three species described by Renault the fibers (prosenchymatous cells) in our specimen are not nearly as prolific as in *C. congenium* or *C. intermedium*. As far as the wood sector-fiber-primary ray relationship is

concerned it compares much more closely with *C. striatum*. However, the Kansas fossil shows somewhat less fibrous tissue than *C. striatum* and the rays of *C. americanum* appear less regular; that is, they tend to be more frequently interspersed with fibrous cells than is indicated by Renault's fig. 5 (1898). An additional difference is the very elongate, almost scalariform tracheidal pitting reported in *C. striatum*, whereas *C. americanum* has the multiseriate-bordered type, presenting a striking contrast.

Diagnosis:

Pith area small, about 3.5 mm. diameter; primary rays flanked on either side by 3–5 rows of fibrous cells which also occur interspersed in the primary rays; fibrous cells with thicker walls than tracheids and smaller diameter; some small rays present in the wood sectors; tracheids with multiseriate circular bordered pits in radial walls.

Horizon and age: Fleming coal, upper part of the Cherokee shale, Missouri series, mid Pennsylvanian.

Locality: from strip mine located about four miles south of West Mineral Kansas.

Type specimen: No. 709, Henry Shaw School of Botany, Washington University, St. Louis.

Arthroxylon Reed, 1952

The curious taxonomic history of the fossils now included in this genus is given by Miss Reed in the preceding article.

Arthroxylon Williamsonii Reed

The following description is based on several stem specimens collected by Dr. A. H. Blickle at the Argus coal mine two miles north and three miles east of Oskaloosa, Iowa. Associated with them were several other coal balls containing calamitean roots. It seems very likely that these are the roots of this species but organic connection thus far has not been proven. Another specimen of *Arthroxylon* (No. 750), obtained from the West Mineral, Kansas, locality, is probably referable to this species. There is, however, an element of doubt involved and when additional specimens are discovered, it may be necessary to recognize this as a distinct species.

When viewed in transverse section, *Arthroxylon* cannot be distinguished from *Arthropitys*. However, in a tangential section the departure of *Arthroxylon* is very striking, the distinction lying in the vertically elongate nature of the cells composing the primary rays (cf. text-figs. 2, 3). This is a character which distinguishes *Arthroxylon* not only from other articulate genera but from all other vascular plants so far as I am aware.

Figure 15 shows in transverse view a representative portion of a stem. In the specimens the primary rays appear appreciably darker than the wood sectors due apparently to slightly thicker cell walls. Although only about 2.5 mm. of sec-

ondary wood are present the primary rays retain their identity essentially unchanged through that distance.

A distinctive feature of the stem lies in the nature of the inner limits of the xylem. The wood sector and primary rays form a very uniform line (fig. 15), that is, the pith does not extend into the xylem between the wood sectors, and the distinctive cellular organization of the primary "ray" is reflected in this sharp demarcation line between pith and xylem. The protoxylary canals thus assume an even more conspicuous position than is usual in the other two genera, and they are bounded on their lateral and inner walls by a layer about two cells deep of relatively small and thick-walled cells.

The primary "rays" are composed of greatly elongate cells which average about 30 μ in diameter and are in excess of 3 mm. long (fig. 19); thus their length is at least 100 times that of their diameter. It is not possible to measure the length accurately but this approximation will suffice to show the striking contrast with the primary ray of *Arthropitys*.

The wood sector consists of two types of cells, the greatly elongate tracheids, and secondary "ray" cells which are also unique in their organization (fig. 20). The latter are smaller than the tracheids, averaging about 30 μ in diameter, and are as long as .5 mm. The size and organization of these cells vary considerably, however. A ray may consist of a single cell which may be as little as .15 mm. long or as tall as .3 mm., but most of the rays consist of several cells each ranging from .3 to .5 mm. tall, and the ray as a whole may be several mm. tall. When observed in a perfect radial section (fig. 18) they present the storied effect found in certain dicotyledons.

Roots Associated with Arthroxylon Williamsonii.—

The calamitean roots have been dealt with in some detail by Renault (1885) and by Williamson and Scott (1895). These authors have pointed out their distinct characters but we still know very little about the respective identity of the roots of the three stem genera.

Williamson and Scott cite the following characters which in general serve to distinguish the roots from the stems:

1. Centripetal development of the primary xylem.
2. Alternate arrangement of the primary groups of xylem and phloem.
3. Endogenous mode of origin of the organ itself and of its branches.
4. Absence of nodes.

To which the following may be added:

5. Absence of protoxylary canals.
6. Greater abundance of pith tissue.
7. Absence of conspicuous primary rays.

It is evident that these seven characters are neither infallible nor always useful. The centripetal development of the primary xylem is certainly distinctive in most cases but, as I have pointed out above, there is reason to believe that this was

present in some of the stems. The arrangement of the primary xylem and phloem groups is of course only of use when very young and well-preserved specimens are at hand. With reference to the third point, it is by no means easy to determine the exact anatomical origin of these organs. Judging from the few stem specimens that I have examined with roots in organic connection[3], the branch stems arise much more regularly (that is, in distinct whorls) and depart more directly than do roots. The absence of nodes appears to be a good character but of course may not be useful in a small fragmentary specimen. The absence of protoxylary canals is a striking character and a good one even though these canals are occasionally missing in the stem. Usually the roots display a solid parenchymatous pith in contrast to the central chamber of the stems; in some instances, however, the pith of the roots may be very small, consisting of a half dozen cells or less.

Renault (1885, 1896, 1898) has identified the roots of *Arthropitys* and *Calamodendron*, and although there is perhaps no reason to doubt his correlation with these stem genera no really distinctive characters are cited which would allow one to readily distinguish isolated root specimens.

Astromyelon sp.

Our Iowa specimens range up to nearly 2.5 cm. in diameter although only the xylem and pith are preserved (fig. 27). They all certainly represent one species and their intimate association with the *Arthroxylon Williamsonii* stems strongly suggests that they belong to that plant. No other calamitean stem species have been found in the collection.

Large primary rays, so characteristic a feature of most calamitean stems, are lacking (figs. 27, 28). The pith extends out into the wood (fig. 27), producing an apparently close but superficial comparison with the stem. That is, what appear to be short, broad primary rays here are clearly pith cells, and the transition at their periphery to the secondary xylem is abrupt. It is evident from the transverse section that rays are present in the secondary wood but they are for the most part only one cell wide.

The pitting in the tracheids of these roots is imperfectly preserved but when present at all it appears to consist of rather small circular pits with occasionally elongate ones in evidence. When the roots are viewed (fig. 28) in tangential section the rays are seen to be both numerous and variable in size. A ray may consist of a single small cell or of many relatively large ones, with nearly every conceivable intermediate form.

We are in need of a thorough study of the calamitean roots which will shed light on the comparative anatomy of those borne by the three stem genera considered above. With the abundance of material that is now being collected this should be possible within a very few years. There are, however, some interesting structural differences between the wood of these roots and that of *Arthroxylon Williamsonii* which may be noted.

[3] Roots have been observed with stems of *Arthropitys communis* var. *septata*, but sufficient material has not been available to make a comparison with the roots described here.

A fundamental character which appears to distinguish the two in most if not all cases is the absence of the primary rays in the roots. I feel that a distinction may be drawn between primary rays (which are so characteristic of the stems; see figs. 10, 14, 16, 29) and the pith "bays" of the roots (fig. 27). The latter may be rather deep (see, for example, Scott, 1920, fig. 16) but usually they are not and the "bay" ends abruptly. Beyond this point the wood is homogeneous, consisting of an admixture of tracheids and small rays. The general appearance approaches rather that of the peripheral region of an *Arthropitys* stem species whose primary rays tend to lose their massive identity. In general, however, the secondary wood anatomy of the stem and roots appears to be quite distinct.

If the secondary wood structures of our *Astromyelon* (fig. 28) be compared with the wood of the associated stems of *Arthroxylon Williamsonii* (figs. 19, 20) the difference is quite striking. *Astromyelon* presents a more or less uniform admixture of tracheids and small rays comparable with the wood sector of an *Arthropitys* (fig. 11). This is very different from the secondary wood anatomy of *Arthroxylon* as described above and as illustrated in figs. 19, 20.

Further speculation is not justified at present but, assuming that the roots found associated in the Iowa coal balls were borne by *Arthroxylon Williamsonii*, it would appear that the roots have retained the more normal ray structure (as displayed in *Arthropitys*), while the striking specialization of secondary tissues has been confined to the stems.

An Arthroxylon Specimen from West Mineral, Kansas.—

A specimen of *Arthroxylon* has recently turned up in our collections from the West Mineral, Kansas, locality which will be briefly mentioned here chiefly because its size is appreciably greater than that of the Iowa and Indiana specimens.

The wood attains a thickness of 18 mm. The distinction between the wood sector and primary ray is sharply defined in transverse section and remains uniform. Like in the Iowa specimens, however, the transverse view does not reveal the unique nature of the primary rays. The protoxylary canals measure about 300 μ in diameter. The wood sectors measure about 1.4 mm. wide and the primary rays about .8 mm.

In tangential section the primary "ray" cells appear to be as long as the tracheids and have essentially the same gross morphology. Occasionally, however, a vertical row of cells will be observed with transverse walls, the cells being 10–12 times as long as broad. I have observed no pitting in the walls of either of these two types of cells composing the primary ray.

The wood sector consists of tracheids which seem to be predominantly of the reticulate-bordered type with an occasional tendency toward scalariform. Scattered sparsely through the tracheids are uniseriate rays most of which are only 3–4 cells high but a few have been observed which are 2–3 times as tall as that. The component cells are variable in size and shape. They tend to be squarish or vertically elongate, and may vary in a single ray from 84 $\times$ 48 μ to 350 $\times$ 50 μ, the first dimension in both cases being the vertical one.

Acknowledgment.—

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Explanation of Plate

PLATE 18

Arthropitys communis (Binney) Hirmer & Knoell, var. *septata* Andrews

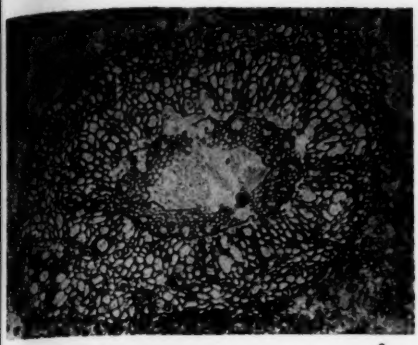
Fig. 1. Inner portion of the wood and peripheral pith region in transverse section. Coal ball No. 722. Peel 722-C4-1. × 9.

Fig. 2. Transverse section of a portion of the stem showing the extent of secondary growth. Coal ball No. 722. Peel 722-C4-20. × 5.

Fig. 3. Tangential section showing a departing branch stele. Coal ball No. 722. Peel 722-C5a-4. × 10.

Fig. 4. A small stem from the Berryville, Illinois, locality, possibly referable to *A. communis* var. *septata*. Slide 1969. × 32.

Fig. 5. Tangential section of a wood sector near the pith showing the septate nature of the tracheids. Coal ball No. 722. Slide 1931. × 140.



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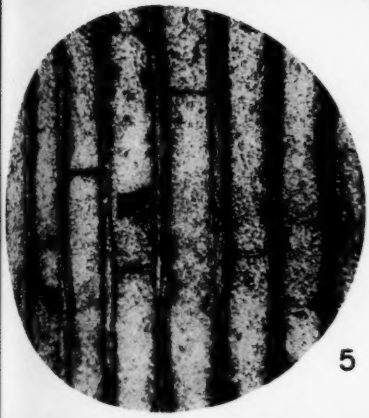

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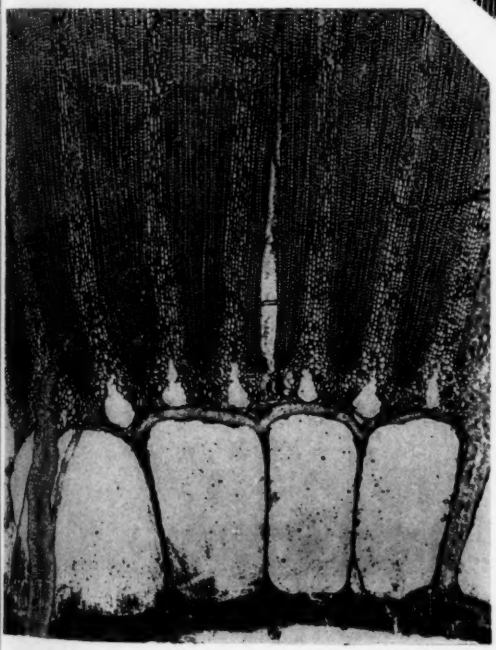

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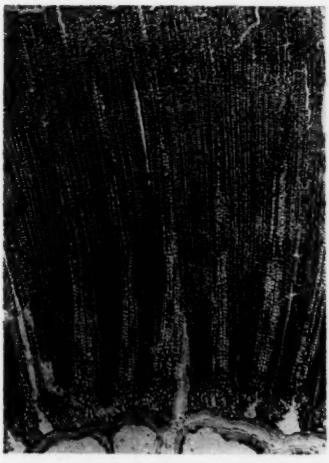


ANDREWS — PETRIFIED CALAMITEAN STEMS

Explanation of Plate

PLATE 19

Arthropitys communis (Binney) Hirmer & Knoell, var. *septata* Andrews

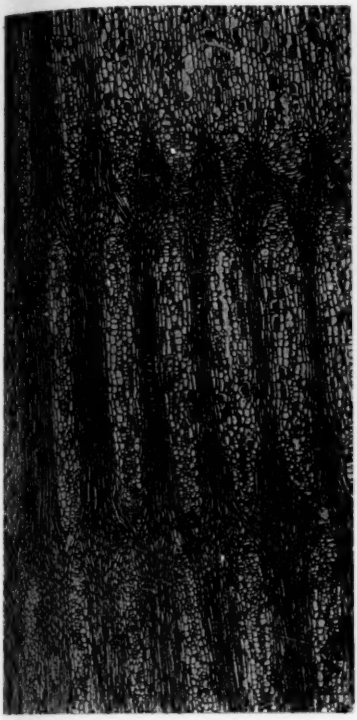
Fig. 6. Tangential section of stem near pith. Coal ball No. 722. Peel 722-C2-15. × 9.

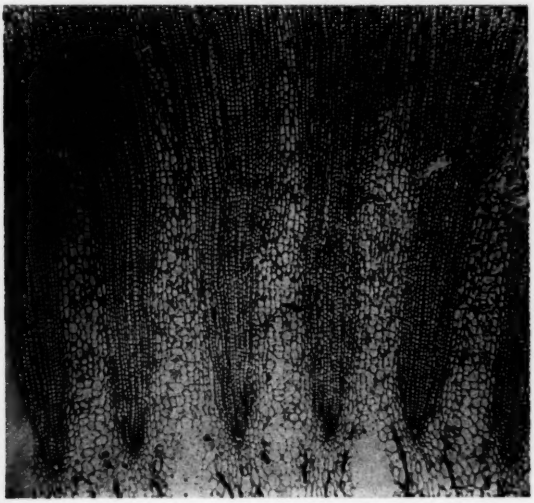
Fig. 7. Tangential section of stem several mm. from the pith (see text). Coal ball No. 722. Peel 722-C2-2. × 9.

Fig. 8. Scalariform pitting in radial walls of tracheids. Coal ball No. 722. Slide 1931. × 145.

Fig. 9. Radial view of secondary ray in wood sector. Coal ball No. 722. Slide 1931. × 46.

Fig. 10. Portion of stem in transverse section. Coal ball No. 804. Slide 1948. × 13.





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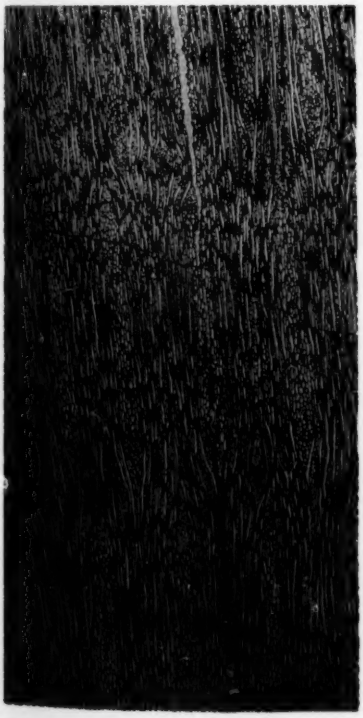

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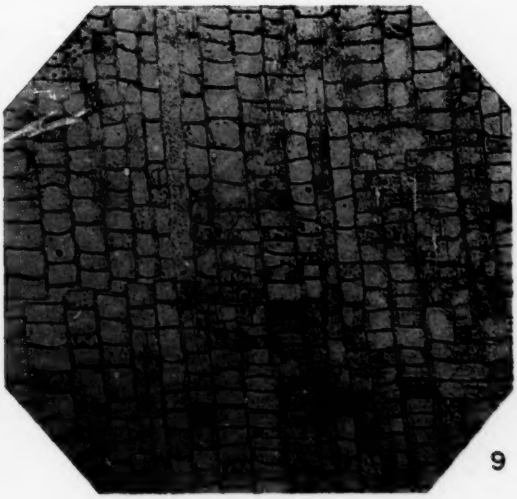

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ANDREWS — PETRIFIED CALAMITEAN STEMS

Explanation of Plate

PLATE 20

Arthropitys kansana Andrews

Fig. 11. Tangential section showing two narrow primary rays. Coal ball No. 786. Slide 1920. × 34.

Fig. 12. Pitting in radial walls of tracheids. Coal ball No. 786. Slide 1921. × 110.

Arthropitys communis var. *septata* Andrews

Fig. 13. A small stem from the locality of Berryville, Illinois. Slide 1968. Coal ball No. 756. × 20.

Fig. 14. A portion of the stem in transverse section. Coal ball No. 755. Peel 755-A-b2. × 7.

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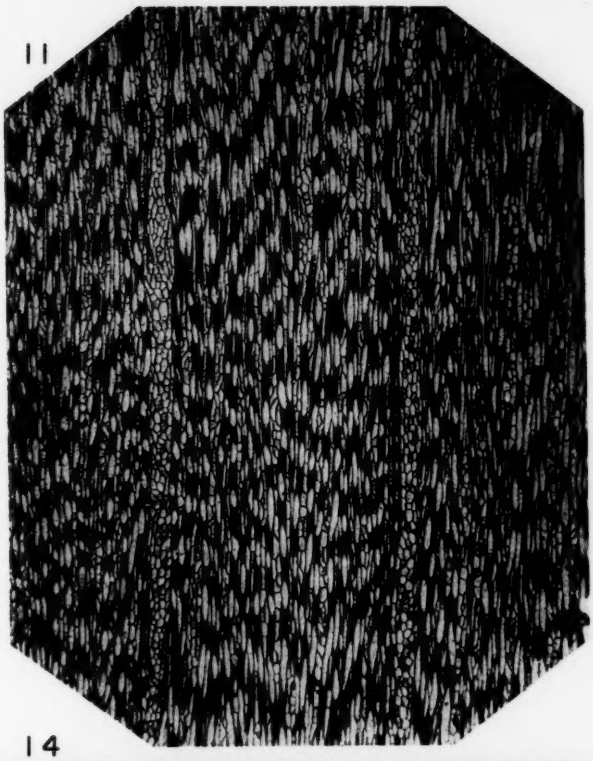

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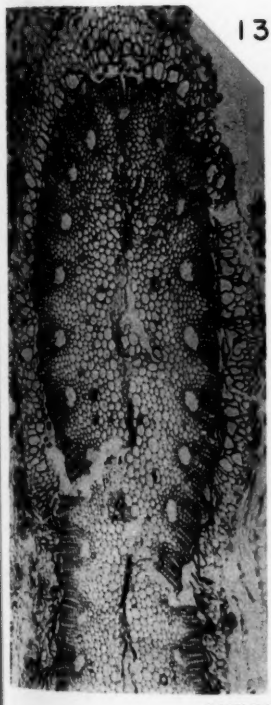

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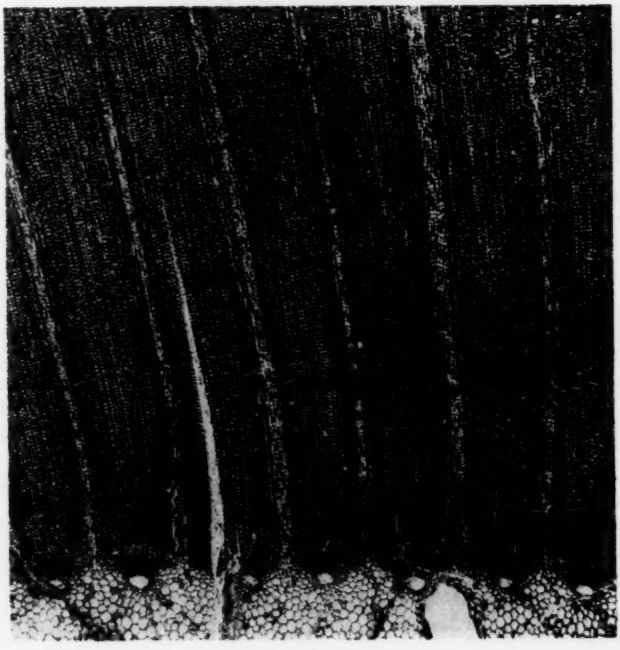

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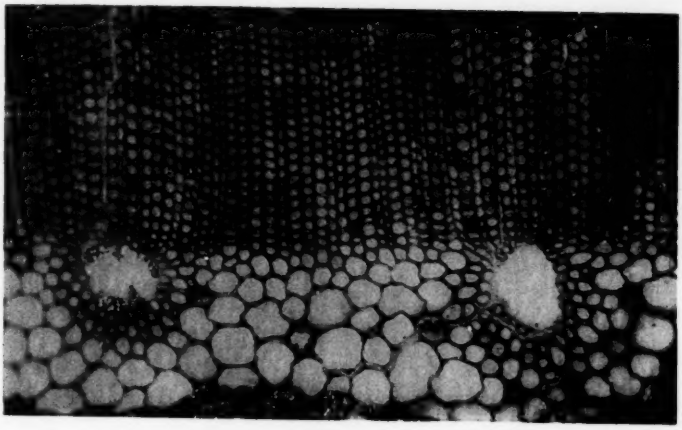
ANDREWS — PETRIFIED CALAMITEAN STEMS

Explanation of Plate

PLATE 21

Fig. 15. *Arthroxylon Williamsonii* Reed. A portion of the stem in transverse section. Coal ball No. B30. Slide 1972. × 60.

Fig. 16. *Arthropitys* sp. A. A portion of the stem in transverse section. Coal ball No. 805. Slide 1955. × 14.



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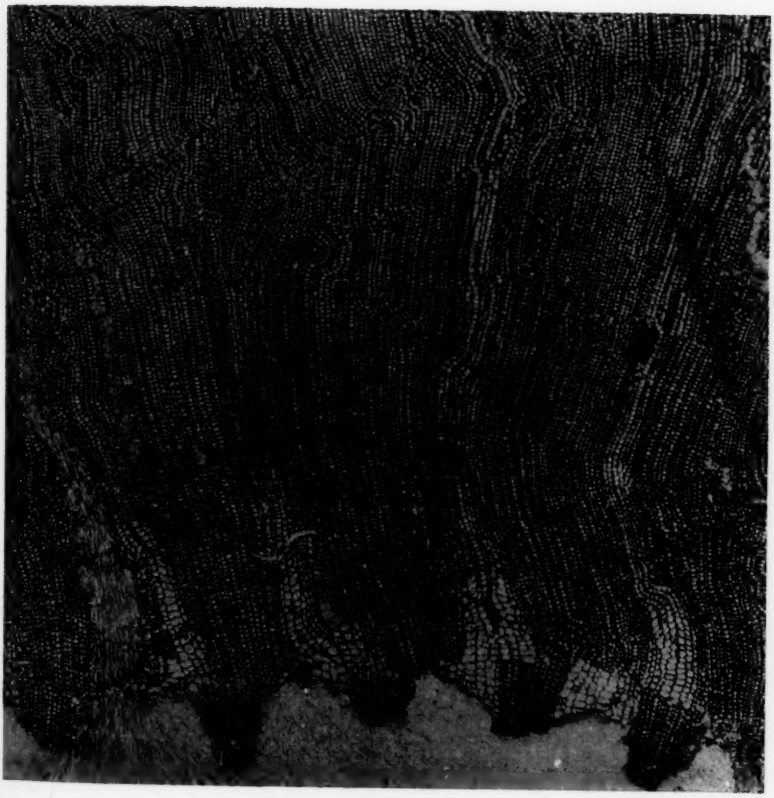

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ANDREWS — PETRIFIED CALAMITEAN STEMS

EXPLANATION OF PLATE

PLATE 22

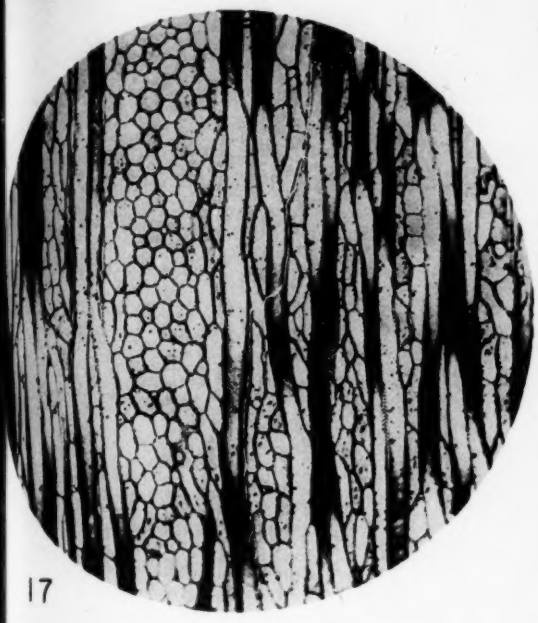
Fig. 17. *Arthropitys kansana* Andrews. Tangential section of the wood enlarged showing one primary ray and numerous secondary rays in the wood sector. Coal ball No. 786. Slide 1920. × 50.

Arthroxylon Williamsonii Reed

Fig. 18. Radial section of a secondary ray of the wood sector. Coal ball No. B3. × 65.

Fig. 19. Tangential section of the stem showing a primary ray (dark) with portion of a wood sector on either side. Coal ball No. B3. Slide 1973. × 60.

Fig. 20. A wood sector in tangential section showing the vertically elongate nature of the secondary ray cells. Coal ball No. B3. Slide 1973. × 74.



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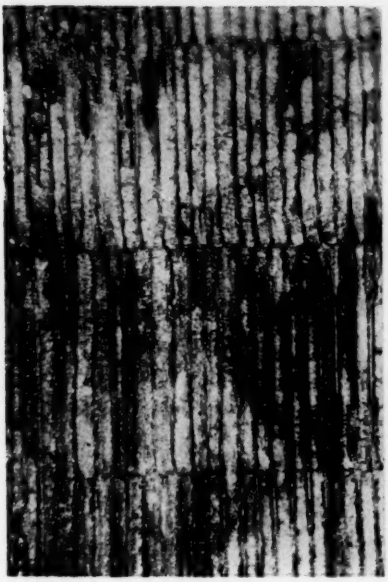

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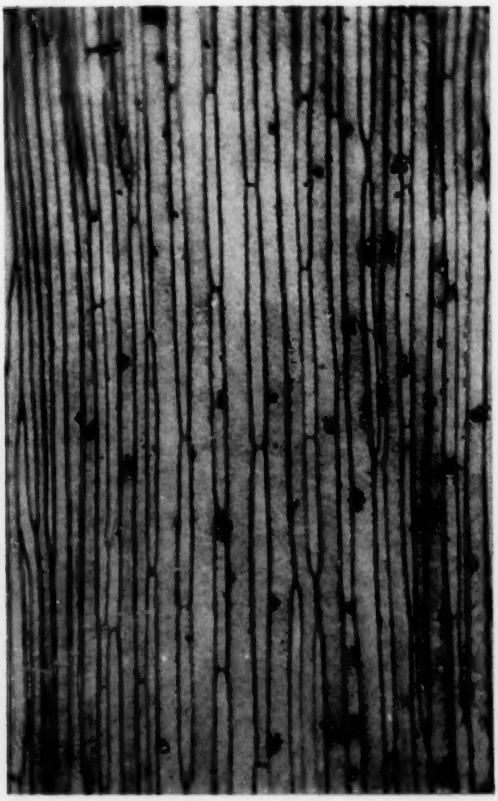

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ANDREWS — PETRIFIED CALAMITEAN STEMS

EXPLANATION OF PLATE

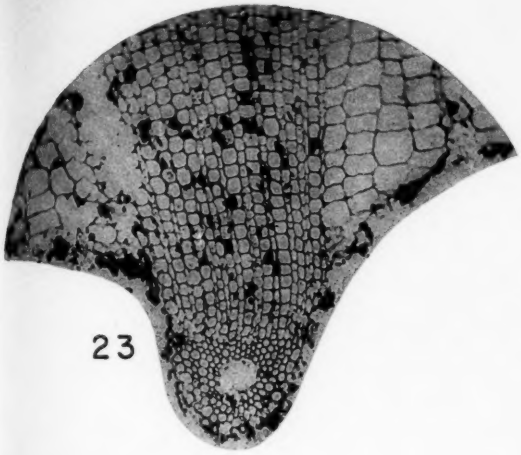
PLATE 23

Figs. 21, 22. *Arthropitys* sp. B. Pitting in radial walls of tracheids. Coal ball No. 753. Slide 1924. × 175.

Figs. 23, 24. *Arthropitys* sp. A. Showing thick-walled cells (centripetal tracheids?) on inner side of protoxylary canal. Coal ball No. 805. Slide 1955. × 40.

Fig. 25. A single protoxylary group of the root shown in fig. 27. Coal ball No. B30. Slide 1942. × 37.

Fig. 26. *Arthropitys kansana* Andrews. Radial view of secondary ray of wood sector. Coal ball No. 755. Slide 1915. × 50.



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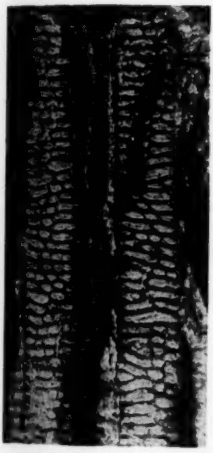

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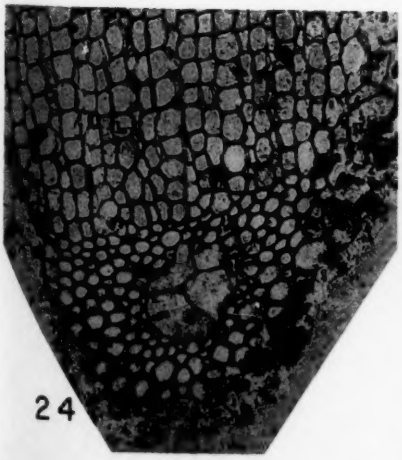

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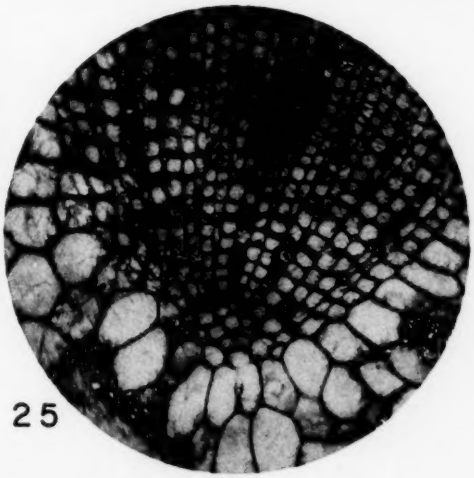

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ANDREWS — PETRIFIED CALAMITEAN STEMS

EXPLANATION OF PLATE

PLATE 24

Astromyelon sp., probably root of *Arthroxylon Williamsonii* Reed

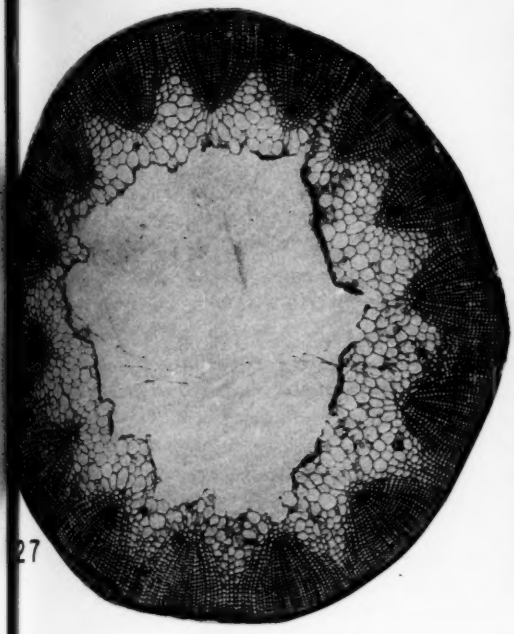
Fig. 27. Transverse section. Slide 1942. × 7.5.

Fig. 28. Tangential section. Slide 1976. × 16.

Calamodendron americanum Andrews

Fig. 29. Transverse section. Peel 709-B-t 6. × 11.

Fig. 30. Tangential section showing a primary ray flanked by the fibrous cells characteristic of this genus. A fiber cell may also be noted running through the middle of the ray. Slide 1913. × 100.



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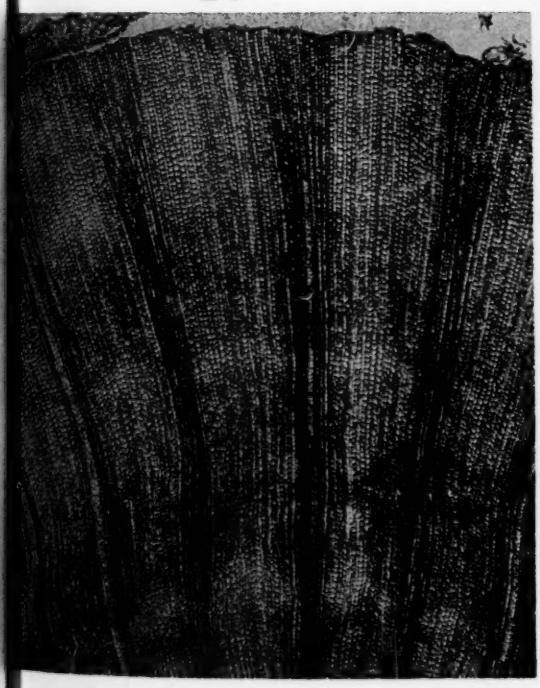

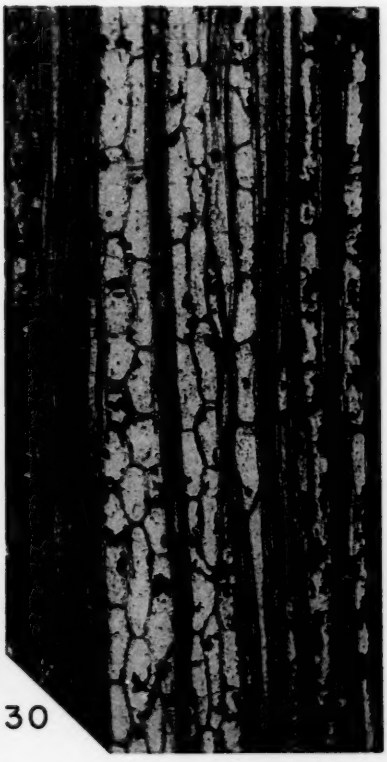

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ANDREWS — PETRIFIED CALAMITEAN STEMS

VARIATION IN THE PERFOLIATE UVULARIAS*

ROBERT A. DIETZ**

In New England and New York, where the two perfoliate species of *Uvularia* are found, little difficulty is encountered in distinguishing them. Although both species in that area vary somewhat, *U. perfoliata* is small and glabrous, while *U. grandiflora* is distinctly larger and its leaves are pubescent on the lower surface. However, southward along the western border of the distribution of *U. perfoliata*, the variation within both species becomes so marked that for occasional collections the accepted criteria for distinguishing them breaks down. In the perfoliate species of *Uvularia*, variants more or less difficult to classify are most commonly found along a line roughly extending from Rochester, New York, down the Appalachian Mountains through eastern Tennessee and into northeastern Alabama. For example, while the New England botanist could tell at a glance the species to which a plant from the Berkshires belonged, he would require a hand-lens for classifying them in eastern Tennessee, and even with this aid several plants from a given woodland would probably be termed "special problems."

In order to measure this perplexing variation and to analyze its cause, the present project was undertaken. Mass collections of plants of *Uvularia perfoliata* and *U. grandiflora* were obtained from several collaborators, as listed below,[1] and they were supplemented by further collections made during the course of the investigation. Individuals from these mass collections were measured, the measurements covering the following characters:

Pubescence
Length of longest internode
Number of leaves
Number of fruits
Leaf index (leaf width/leaf length)
Leaf length
Leaf width
Leaf shape
Length of first internode below branch
Length of second internode below branch
Length of third internode below branch
Length of first internode, fertile branch
Length of first internode, sterile branch
Ratio of first internode on fertile branch to first internode on sterile branch
Length of each additional internode, sterile branch
Length of each additional internode, fertile branch
Shape of fruit
Length of fruit pedicel
Number of hairs per square millimeter on lower leaf surface
Length of hairs on lower leaf surface

Wherever the nature of the material permitted, these measurements were treated statistically. The method of pictorialized scatter diagrams was chosen to analyze these data, since it permits several variables to be depicted on a single chart

[1]Edgar Anderson, Missouri Botanical Garden; Reino Alava, Missouri Botanical Garden; Ralph Erickson, University of Pennsylvania; Norman Fassett, University of Wisconsin; Leslie Hubricht, Danville, Virginia; Royal Shanks, University of Tennessee; Stanley Smith, New York State Museum; George Van Schaack, Washington University; H. A. Wallace, South Salem, New York; and Edgar Wherry, University of Pennsylvania. In addition, material was examined in the following herbaria: Cranbrook Institute of Science, Missouri Botanical Garden, New York Botanical Garden, University of Michigan, and University of Pennsylvania.

*An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the degree of Doctor of Philosophy.

**Department of Botany, University of Tennessee, Knoxville.

rather than two, as in ordinary scatter diagrams. The first five characters in the above list were finally adopted for the charted data.

Mature plants were used in all measurements. A plant was considered mature when it had ceased elongating and the terminal leaves were fully expanded. This occurs at some time after the fruit has developed to a point where its mature form is clearly recognizable, two to three weeks after the perianth has fallen off. Depending on the clone and the environment, this may be from late April to mid-June. The plants remain in a "measurable" state from this time until the first autumn frost, except for the fruits, which reach full size about two months after the perianth has fallen.

Since plants in flower have not reached maximum growth, floral characteristics do not appear in the above list, but some discussion of floral characteristics is given later in this paper.

General Characteristics of the Perfoliate Uvularias

The perfoliate species of *Uvularia* constitute a natural division of the genus, and consist of two species, *U. perfoliata* and *U. grandiflora*. These are plants with a short rhizome containing numerous fleshy appendages, an aerial stem bearing

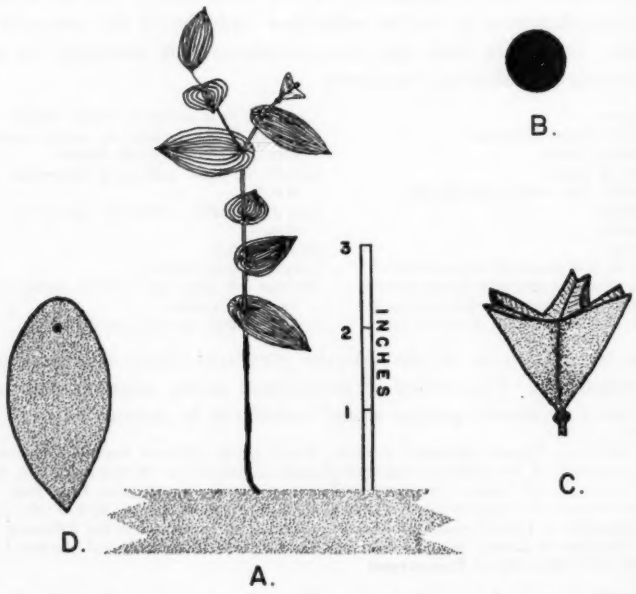


Fig. 1. *Uvularia perfoliata:* A, habit; B, dot as used on charts; C, fruit; D, leaf outline (× 2 habit scale).

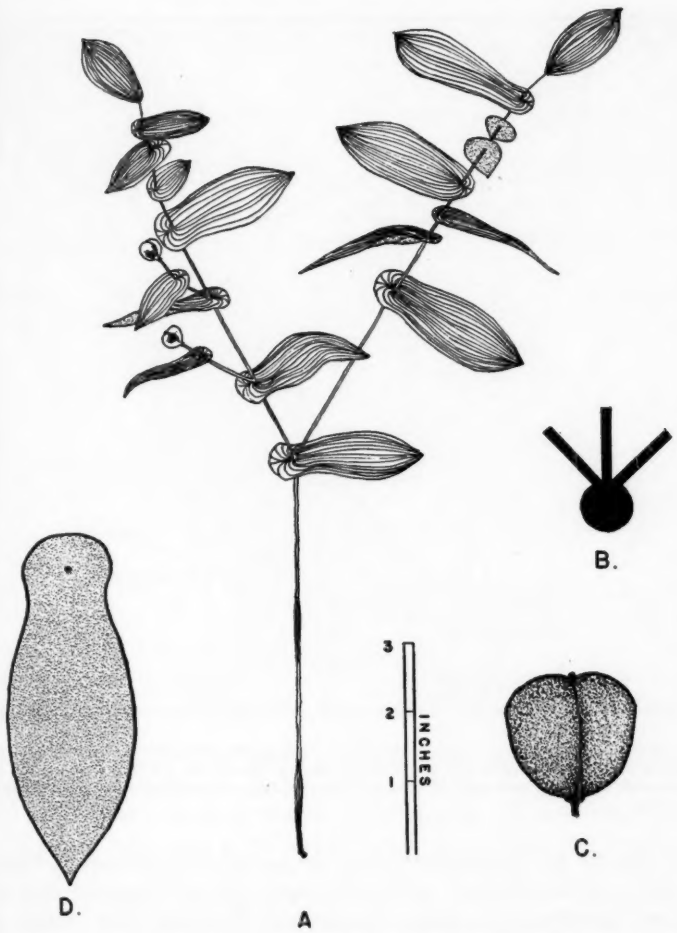
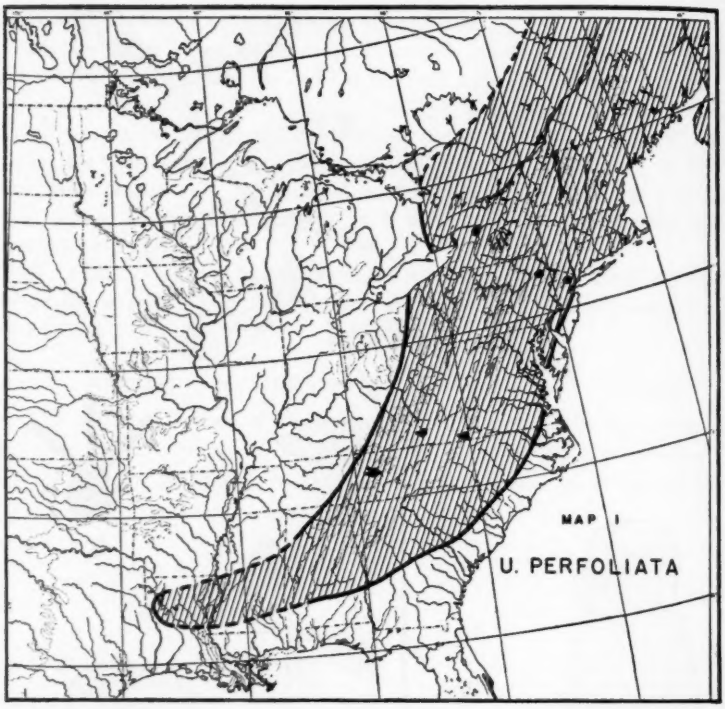


Fig. 2. *Uvularia grandiflora:* A, habit; B, dot as used on charts; C, fruit (about × 4 habit scale); D, leaf outline (×2 habit scale).

3–5 cataphylls below and 6–36 perfoliate leaves above. Mature plants characteristically are branched one or more times, the branching superficially resembling a true dichotomy. One to four flowers may be present on a given aerial stem. These are axillary, and are never borne below the lowest branch. The liliaceous perianth is made up of three yellow petals and three yellow sepals. The flowers droop, never developing the widely spreading perianth segments characteristic of such genera as *Lilium* or *Hyacinthus*. Flowering occurs within a few days to about

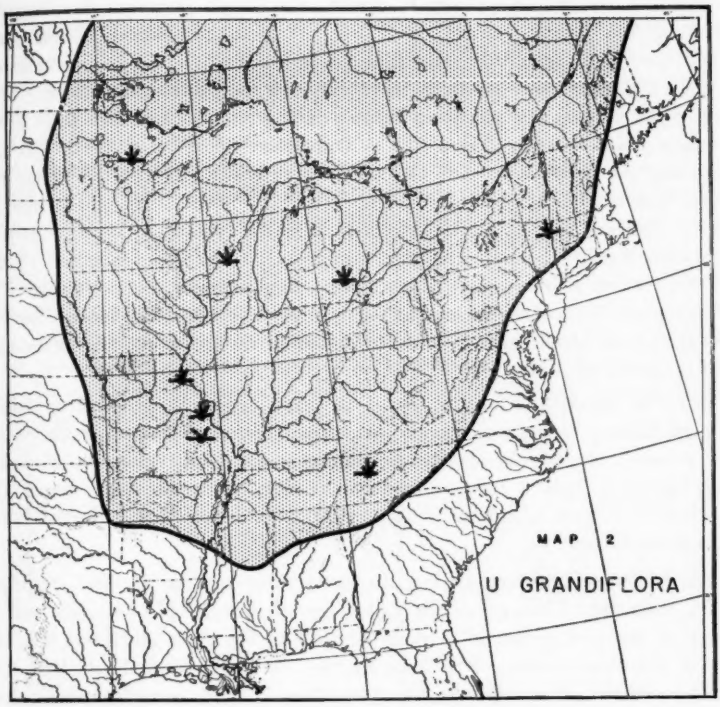


The symbols used on Maps 1 and 2 are similar to those on the charts. An additional pair of rays depicts the values found on the ordinate and abscissa, the ray to the left depicting the longest internode with increasing values to the left; that on the right, the leaf index with increasing values to the right.

a week after the first shoot appears above the ground and consequently before the plants have reached full size. Statistically useful data on vegetative parts of the plant are impossible at this stage. The 3-angled loculicidal fruit contains about 12 round, dark, hard seeds 2–3 mm. in diameter. The capsule shape varies from sharply acute at the tip to moderately obtuse and lobed (fig. 5).

Uvularia perfoliata and *U. grandiflora* are woodland plants, varying in their preference for deep or open situations, soil types, and plant associations. The plants usually persist from mid-spring to mid-autumn. Maximum growth on the aerial stems has occurred shortly after the fruits are large enough to be recognized. The plants used for measurements of vegetative parts in this project were all mature, in the sense that maximum growth had been reached.

Having considered the characteristics of the perfoliate Uvularias as a whole, the intraspecific characters will now be discussed.



Uvularia perfoliata.—This species was established in the first edition of Linnaeus' 'Species Plantarum,' in 1753. It is a small plant, with 5 to 8 leaves of which 3 or 4 are below its single branch. The leaves are glabrous, glaucous, oval and thin; the one subtending the branch is 65 mm. or less long. The longest stem internode, generally found below the lowest leaf, is 100 mm. or less long. The flower-bearing branch has a single leaf that subtends the flower. The single flower is pale yellow. The perianth segments have a granular appearance on the inside caused by rough, many-celled emergences. These are visible to the unaided eye, and under the hand lens are shown to be small papillae. The 6 stamens are as long or shorter than the trifid style. The tips of the anthers are pointed. The three-angled capsule of the fruit is broader than long (each angle two-ridged), the tip acute (fig. 1C).

Uvularia perfoliata is found in rather open woods, in neutral or slightly acid soil, frequently under white oaks and rarely under red oaks. Our collecting experience has been that the species was never particularly abundant in the mature form. Seedlings and sexually immature, non-branching older plants are not uncommon in many white oak woods, but these are nearly useless for comparative purposes.

Uvularia grandiflora.—James E. Smith, the British botanist, described this species in his 'Exotic Botany' in 1804. It is a considerably larger plant than *U. perfoliata,* sometimes waist-high. There is a single leaf below the lowest branch. Generally there are 16 or more leaves on the plant, and there may be as many as 36. These are pubescent below, dark green, thicker than those of *U. perfoliata* and frequently shaped like a "Dutchman's shoe" (fig. 2D). The leaf subtending the branch is 85 mm. or more long, typically 100–130 mm. long. The longest stem internode, generally found below the lowest leaf, is 150 mm. or longer. Flowers may be borne on either the main branch, or on secondary or tertiary side branches, and generally number from 1 to 4. The branches are leafy. The flowers are yellow, somewhat brighter than those of *U. perfoliata.* The perianth segments are smooth on the inside. The 6 stamens are longer than the style, with blunt-tipped anthers. The three-angled capsule of the fruit is obtusely lobed at the tip (fig. 2C).

Uvularia grandiflora usually grows in deep woods, in beech-maple forests or in oak-hickory forests, and there is no apparent preference for red or white oaks. It is generally found abundantly in mature stages. One clone in Michigan, measuring about 5 × 8 feet, contained more than 50 mature aerial stems. On a southern Wisconsin hillside collecting 25 plants made no visible reduction in the apparent abundance.

The following table summarizes the distinctions between *Uvularia perfoliata* and *U. grandiflora.* Because of the high degree of intermediacy along the zone of overlap of the two species, it is more practical to list those characters least like those of the other species. It is intended that the assumption should hold, viz., that the perfoliate *Uvularia* least like *grandiflora* is, in nature, the best *Uvularia perfoliata,* and also the converse must be true.

A COMPARISON OF THE PERFOLIATE UVULARIAS

Uvularia perfoliata (least like *U. grandiflora*)	*Uvularia grandiflora* (least like *U. perfoliata*)
Flower	
Solitary	1–4
Perianth granular-rough within	Perianth smooth within
Stamens equal in length to style or shorter	Stamens longer than style
Anthers pointed at tip	Anthers blunt-tipped
Fruit	
Capsule acutely truncate	Capsules obtusely lobed
Leaves	
Lower surface glabrous	Lower surface strongly pubescent
3 or 4 below lowest branch	One below lowest branch
Branch-subtending leaf 65 mm. or less long	Branch-subtending leaf 85 mm. or more long
5–8 per plant	13–36 per plant
Fertile branch with one leaf	Fertile branch with many leaves
Glaucous	Deep green
Smooth, thin	Rough, thick
Oval	Mature leaves shaped like a "Dutchman's shoe"
Size	
Longest internode 100 mm. or less	Longest internode 150 mm. or more

History of the Perfoliate Uvularias

The perfoliate species of *Uvularia* are sufficiently distinct from other Liliaceae to make their botanical position clear, and, with perhaps one exception, the history of this group does not show that these plants were ever confused with those of closely allied genera. What confusion has existed lies between inter-specific, rather than inter-generic, similarities.

As indicated in the preceding section, *Uvularia perfoliata* is a Linnean species and *U. grandiflora* was established by Smith in 1804. At the same time that Smith established *U. grandiflora,* he described another species from eastern America which he named *Uvularia flava.* Described as rare, *U. flava* was similar to *U. perfoliata* but with deeper yellow flowers and perianth smooth within—floral characteristics which suggest *U. grandiflora. U. flava* was recorded from New Jersey to Virginia, well within the range of *U. perfoliata,* and on the extreme eastern boundary of the distribution of *U. grandiflora. U. flava* appears to have been a hybrid between *U. perfoliata* and *U. grandiflora* and is no longer recognized as a species.

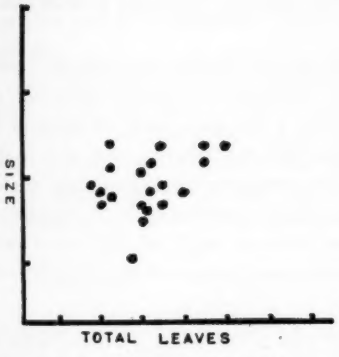


Fig. 3. Knoxville "Collection A"

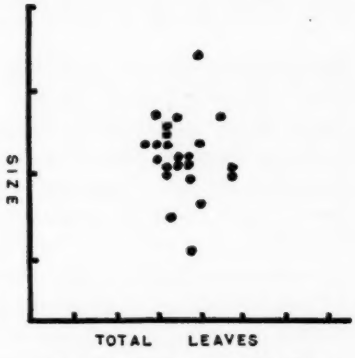


Fig. 4. Knoxville "Collection B"

These scatter diagrams show the size (length of longest internode) plotted against the total number of leaves on the plant. Note the high degree of overlap between the two collections.

Walter's collection of American plants, made in the latter half of the eighteenth century, contained a plant which he called *Anonymos (Erythronio affinis) pudica.* Walter did not collect or identify as such any plants of *Uvularia,* but from the description (Fl. Carol. 1788) his plant undoubtedly refers to a species of that genus. Michaux (Fl. Bor. Am. 1803) considered Walter's specimen to be *U. perfoliata.* In 1833 Asa Gray noted that it resembled the mountain *Uvularia, U. puberula* Michx. Unfortunately, the specimen now appears to be lost; at least it is not in the British Museum where Walter's herbarium is kept. We today have only Walter's description to show what the plant may have been. This reads, in part: "capsula turbinato-triangularis, angulis bifidis, trilocularis, trivalvis," and "foliis amplexicaulibus."

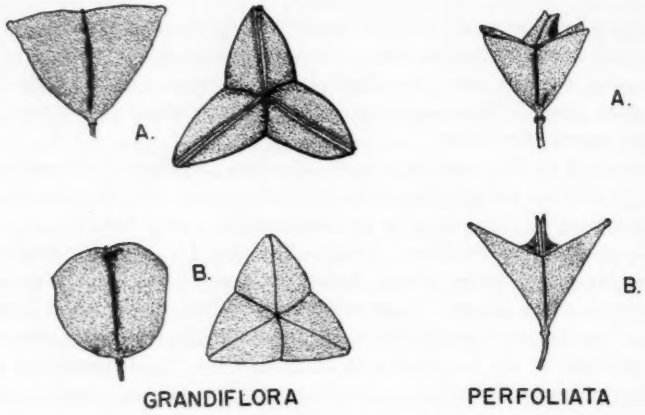


Fig. 5. Capsule types: Left—A and B, Billington; Right—A, Ridgewood; B, Monte Sano.

Fernald (Gray's Manual, 1939) uses this plant of Walter's to establish *Uvularia pudica* (= *Uvularia puberula* Michx.). *U. puberula* is a sessile-leaved plant, and the leaves are not "amplexicaul," although for a few days after the shoot of this plant appears above the ground the leaves *appear* to clasp the stem, due to their folding within the bud. Depending upon the interpretation, the capsules of either *U. puberula* or *U. perfoliata* might be considered "top-shaped." It may be that Walter's plant was a perfoliate *Uvularia*, as Michaux suggested, and not a sessile-leaved form. In any case, it appears that the name *Uvularia pudica* should be discarded and Michaux's *U. puberula* restored.

Nuttall recognized a distinction between the eastern and western populations of the perfoliate Uvularias, apparently without having read Smith's description of *U. grandiflora*. He wrote in his diary on May 14, 1810, in northwestern Pennsylvania, "There is in these swamps also abundance of a plant which I at 1st took to be *Uvularia perfoliata*, but it is much larger than I have usually seen it, the style is trifid nearly to its base; the filaments are very thick subulate & alternately longer."

The various manuals of the flora of eastern North America give the following references to perfoliate species of Uvularia:

Eaton, Amos, *Manual of Botany for North America*. 1833. Eaton notes that *Uvularia flava* equals *Anonymos pudica* Wr., and asks, "Is this distinct from the preceding [*perfoliata*]?"

Wood, Alphonso, *Flora and Class-Book*. 1846. Two species recognized, *grandiflora* and *perfoliata*. Wood notes that *flava* equals *perfoliata*.

Gray, Asa, *Manual of Botany*. 1857. Two species, *grandiflora* and *perfoliata*.

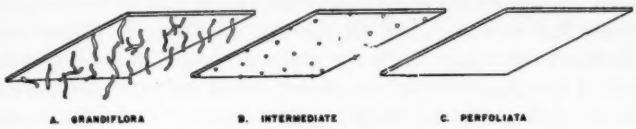


Fig. 6. Vesture types.

Gray, Asa, *Manual of Botany.* 1868. As above, with *flava* added as a distinct species.

Gray, Asa, *Manual of Botany.* 1887. The species name *flava* is dropped and never reappears in our floras.

The variation within the perfoliate Uvularias led Anderson and Whitaker to look for gross genetic differences in the chromosomes of the two species. They found (1934) that the chromosomes were so similar that the variation could not be ascribed to any gross genetic differences. In a short note, Anderson and Hubricht (1943) pointed out that the difference in leaf texture between *U. perfoliata* and *U. grandiflora* could be attributed to cellular differences in the epidermis.

From this brief history of the genus it may be seen that the problems in identification of the perfoliate Uvularias are *U. flava* and Walter's *Anonymos pudica. U. flava* may be attributed to hybridization and *Anonymos pudica* may belong with the perfoliate Uvularias rather than with Michaux's *U. puberula.* The body of this paper, then, will deal solely with the observed variations between *U. perfoliata* and *U. grandiflora,* and an interpretation of these varieties.

Analysis of Variation in the Perfoliate Uvularias

During the course of this investigation, thirty-four collections of population samples from seventeen states and one Canadian province were examined and measured. These mostly represented small collections of one to twelve specimens from any single locality. In fourteen cases, more than a dozen specimens from one locality were available. The data for each collection were transferred to a pictorialized scatter diagram to show the extent of the variation in that population. For example, in Monroe County, New York, four collections were made, three of which contained from six to twelve specimens, the fourth, thirty-five. In each the variation was measured and treated statistically, but only in the fourth collection (Oakwood Park) were the data placed in a pictorialized scatter diagram. As a result, the diagrams reproduced in this paper represent only a portion of the specimens examined and measured, but because they picture those populations from which the largest number of plants was taken, they are perhaps most valuable for determining the extent of variation in the perfoliate species of *Uvularia.*

The Pictorialized Scatter Diagram.—This technique was developed by Anderson and his students (see Anderson, 1948; Hall, 1952; Sauer, 1951) in their studies

on variation. It has an advantage over conventional scatter diagrams or graphs in that more than two characters (in this case five) may be plotted on a given set of coordinates. For diagrams in this paper, the length of the longest internode (a measure of the plant's height) is plotted on the ordinate, and the leaf index (ratio of leaf width to length; shape) on the abscissa. For a given specimen, a dot corresponding to the length of its longest internode plotted against its leaf index is placed on the chart, as in conventional scatter diagrams. From this dot, rays emanate in various positions and of varying lengths to denote other character measurements. Figure 2B illustrates this construction as applied to *U. grandiflora.* There are three rays. The center one, which stands straight up, represents the number of fruits on the plant. Where there is only 1 fruit, the ray is absent; where there are 2–4, the ray is drawn full length. The ray angling out to the left of the central one denotes the total number of leaves on the plant. Where there are 9 or less leaves, this ray is absent; where there are 10–12, the ray is very short; 13–15 leaves brings the ray out to half-length, and 16–36 leaves are marked by a full-length ray. The third ray, angling off to the right of the central arm, denotes pubescence on the lower leaf surface. An absence of this ray indicates no hairs; intermediate pubescence is shown by a line of half length; and full pubescence is shown by a full-length ray.

Charts 1 and 2 were made from herbarium specimens in the Missouri Botanical Garden. Chart 1 shows *Uvularia perfoliata,* and chart 2, *U. grandiflora.* The herbarium contains more than 200 specimens of perfoliate species of *Uvularia,* but most of these could not be measured either because they were flowering and therefore not fully grown, or they were fragmentary, or they were seedlings. All measurable plants were placed on the charts.

Uvularia perfoliata falls largely in the lower left-hand corner, and consists of dots with no arms or very short arms. The three aberrant examples with one or more long arms in chart 1 are special cases. They are all located in the southern part of the range (southern Virginia, Georgia, and Alabama) where variation in this species tends to be greater, as will be shown below. *Uvularia grandiflora,* on the other hand, tends to occur in the upper right-hand corner of the chart, and the dots are generally long-rayed.

These charts, then, reveal what is already well-known, that is, that *Uvularia perfoliata* is in general a small plant, has few leaves which are wide with respect to their length, a single fruit, and no pubescence. *Uvularia grandiflora* is larger, has many leaves which are narrower with respect to their length, more than one fruit, and is pubescent on the lower surface of the leaf. The distinctions are usually clear, indicating that the two are "good" species.

Preliminary examination of the perfoliate Uvularias, however, showed that a few populations were so intermediate that their identification was made only with difficulty, and when made it might still be open to some question. Shifting measured characters from the ordinate to the abscissa to the rays of the dots, as

well as using other characters than the five finally adopted, were tried before the final form of the charts was decided upon. This final form is an attempt to stress significant differences, in order to separate the species as far as possible, both in their position on the chart and in the number and length of the rays on the dots. As an example of this, when a collection of *U. perfoliata* and of *U. grandiflora* from two different locations near Knoxville, Tenn. were first examined, their similarity, except for pubescence, was most marked. One experiment in chart construction plotted the length of the longest internode on the ordinate against the total number of leaves on the abscissa. So plotted, the charts of each population almost exactly coincided spatially (figs. 3, 4). In the final chart form adopted, there is greater separation (charts 8, 9).

Keeping in mind the intermediacy of some collections, plants whose position on the chart fell in the lower left-hand corner and which consisted of dots with few or no rays, were considered as being less like *grandiflora* rather than more like *perfoliata*. In practice, these mean much the same thing, but in designating specimens as "less like *grandiflora*" or "less like *perfoliata*," depending on whether they fell in the lower left corner and had no rays or in the upper right corner and had long rays, we avoid the danger of setting up arbitrary standards for a species which might conceivably be at variance with the standards set up by the original describer for his type specimen. A "type" may, after all, not be "typical" of the species, yet taxonomically we cannot ignore the standards established by it on this account alone. Therefore, in analyzing the charts, we shall start with those populations least like *grandiflora* and conclude with those least like *perfoliata*.

Ridgewood, N. J. (Chart 3).—This locality is about the center of the range of *U. perfoliata*. The plants collected had invaded a rock garden in an essentially little disturbed residential area which was once a beech woods. They were not planted there, and the owner was ignorant of their presence. It might be observed that they were found in the course of a collecting trip which eventually covered over 4,000 miles, and, oddly enough, they were less than 30 feet from the kitchen door of the home of the writer's parents, a pleasant surprise to him on the halfway spot in an often discouraging trip.

All but three plants from this population were small, had 9 or less oval leaves, a single fruit, and no pubescence. The population was, in fact, less like *U. grandiflora* than any other charted. Three plants had 10 leaves, exhibiting to a very slight degree the leafiness characteristic of *grandiflora*. One plant had 2 fruits—quite unusual for *perfoliata*. In the sense that they were least like *U. grandiflora*, the Ridgewood population was the "best" *U. perfoliata* obtained in the mass collections. There is no indication that the variation is due to anything other than environment and normal heredity.

Hawley, Pa. (Chart 4).—Like the Ridgewood population, less than 100 miles away, this eastern Pennsylvania collection is in the middle of the range of *U. perfoliata*. The forest in which they were found contained areas of white oak predominance and areas of red oak predominance. The plants were found only in

the white-oak areas. There were about half a dozen sterile plants and seedlings for every fruiting plant, unlike Ridgewood where 16 of 23 plants were in fruit. The population is more variable than the preceding one with respect to leaf shape and height, but only one specimen had more than 9 leaves (it had 11) and none had more than one fruit.

In the same forest at the same time, but some distance from the previous population, in a ravine and near a creek, *Uvularia sessilifolia* was collected. The plants of *U. perfoliata* from Hawley do not show any indication of ever having formed hybrids with that species. There is some evidence that a *U. grandiflora* × *U. sessilifolia* cross has been successful in nature (see Red Lake, Minnesota), and that a *perfoliata* × *grandiflora* × *puberula* cross (the latter a sessile-leaved *Uvularia*) has occurred in Alabama (see below). It is, therefore, noteworthy that a *Uvularia* cross apparently did not occur at Hawley where two species occur together.

The high incidence of sterile (*i.e.*, non-flowering) plants in proportion to the fruiting ones was not uncommon in the collections of *perfoliata* made during this study. Plants of *U. perfoliata* were usually found spread out over a rather wide area, and only a small percentage of them were fruiting. *U. grandiflora*, on the other hand, was usually growing in tight colonies, with nearly all the plants fruiting (see Billington Woods, Mich.).

Dyestone Creek, Va. (Chart 5).—These plants were collected along the base of Smith Mountain, Pittsylvania County, on the southern border of Virginia. They are larger plants than those preceding. Nine plants (25 per cent) have more than 9 leaves; six plants (17 per cent) have the longest internode more than 100 mm. long; and one plant has 13 leaves and 3 fruits. The plant with 3 fruits and 13 leaves looks very much like a *U. grandiflora* except for its lack of pubescence.

Mountain Lake, Va. (Chart 6).—This population was located in Giles County, about 100 miles west of the Dyestone Creek population, on the grounds of the University of Virginia Mountain Lake Biological Station. An elevation of about 4000 feet makes the climate more like that in the more northern areas of *U. perfoliata* distribution, although the summer day length is, naturally, somewhat shorter. The collection was made east of the camp site. *U. perfoliata* was growing interspersed with *U. puberula*. For *U. perfoliata*, these were unusually tall plants, eight plants (61 per cent) being found with the longest internode more than 100 mm. Six plants (46 per cent) had 10 or more leaves.

Oakwood Park, N. Y. (Chart 7).—Located in Monroe County, on the east side of Irondequoit Bay, north of Rochester, Oakwood Park (apparently the name of a real-estate development) is near the western boundary of the range of *U. perfoliata*. Although the plants found here are small, like most of that species, the leaves are narrower than usual with respect to their length. Nineteen plants (54 per cent) exhibit a curious intermediate pubescence on the lower surface of the leaves (fig. 6B). Eight plants (23 per cent) have 10–12 leaves. The same intermediate

pubescence is found in two smaller *U. perfoliata* populations collected in Rochester. In the southwest portion of Monroe County a population containing both *U. perfoliata* and *U. grandiflora* was collected. *U. grandiflora* is reputed to grow around the shores of Irondequoit Bay, although none was found during a brief visit in 1951.

In many respects the Oakwood Park collection represents a high degree of intermediacy between *U. perfoliata* and *U. grandiflora*. This point is elaborated in the discussion following the presentation of charted data.

Knoxville, Tenn., Collection "A" (Chart 8).—A population was collected from the University of Tennessee farm woodlot about one mile south of the University campus, by R. E. Shanks. He described the situation as an open canopy with a heavy ground cover dominated by *Rhus, Laportea,* and *Galium*. This population will be discussed in conjunction with the following one.

Knoxville, Tenn., Collection "B" (Chart 9).—This sample was collected on the same day as the preceding one by Dr. Shanks from a wooded slope on the University farm. It was found under a heavy canopy of mixed deciduous trees, in a ground cover rich with *Trillium, Hepatica, Disporum, Polygonatum, Smilacina,* and *Viola*.

These populations represent our best mass-collection data on the perplexing problem of intermediacy. From a casual inspection, the plants from both collections appear to be *Uvularia grandiflora*. Closer inspection reveals that collection "A" consists of plants with leaves glabrous underneath. Still closer inspection shows that one plant of collection "A" possesses a single leaf with full-length hairs near the base on the underside. When this particular sample is under the binocular dissection microscope, the visible field is in no way different from that characteristic of *U. grandiflora*, although the rest of the leaves when viewed under the microscope are characteristic of *U. perfoliata*.

The label for collection "A" states that it is a population of *U. perfoliata*, while that for collection "B" states that it is a population of *U. grandiflora*. There is no question but that collection "B" consists of essentially *U. grandiflora* plants. However, when Chart 9 is compared with the charts which follow, the Knoxville *U. grandiflora* plants are found to be rather uniformly smaller than is typical for that species and are generally less heavily fruited. In addition, only six plants (19 per cent) have as many as 16 leaves, and five plants (16 per cent), have 12 or less. In short, the Knoxville *U. grandiflora* plants plot out on the chart as a group somewhat closer to typical *U. perfoliata* than any other group of *U. grandiflora*.

Collection "A" is a more questionable population. These plants exhibit characteristics of both species. As a group, they lean perhaps more toward *U. perfoliata* than toward *U. grandiflora*. The rather large size of the plants, and the leaf shape as reflected in the leaf indices, is more like *grandiflora* than *perfoliata*. Similarly, eight plants (40 per cent) have 13 or more leaves, and only six plants (30 per cent) have 9 or less leaves. The population is, therefore, leafier than is usual in

U. perfoliata. On the other hand, with the exception noted, the plants have the typical glabrosity of *U. perfoliata.* In another characteristic, not plotted on the chart, twenty plants (100 per cent) had 2 or more leaves below the primary branch, and seven of these (35 per cent) had 3 or more. This leafiness below the primary branch is characteristic of *U. perfoliata.* Collection "B" exhibited more of this characteristic than is usual in *U. grandiflora,* but not to the degree of collection "A."

Both Knoxville collections, then, represent intermediate plants. In collection "B" the taxonomic classification is not difficult; collection "A" is more of a problem. This area is used by classes of the University of Tennessee for ecological studies. It is a valley, rather wet at the bottom, with sloping hills delimiting it. Collection "A" was made on the bottom lands and collection "B" on the hillside, each in a distinct environment. Ordinarily one might expect to find *U. grandiflora* populations in moister locations than those of *U. perfoliata,* but the *grandiflora* populations were from the hillside of the campus and the *perfoliata* collection in the moister bottom area.

Debbink, Oconomowoc, Wisc. (Chart 10).—Near the shore of Lac La Belle, Oconomowoc, *Uvularia* was growing under an open canopy of *Tilia, Ulmus, Acer,* and among *Smilacina, Podophyllum, Pteris,* and *Equisetum.* Although clearly *U. grandiflora,* plants in this collection are smaller than usual for this species, and the leaf shape is quite variable. Only three plants (12 per cent) have more than one fruit. Ten plants (40 per cent) have less than 16 leaves, although one plant has 27. The leaf color of the fresh specimens was quite variable, ranging from deeply bluish-green, through dark green to yellowish-green.

La Barque Creek, Mo. (Chart 11).—Found in mixed woods at the base of a sandstone bluff in the La Barque Creek area south of Eureka, Missouri, this collection consists of moderately large plants with narrower leaves than usual for *U. grandiflora.* Notable in this population is the complete absence of plants with more than one fruit. *U. sessilifolia,* like *U. perfoliata,* is typically a single-fruited plant. It is found in Missouri, although more frequently north of the Missouri River than south of it.

Butts, Mo. (Chart 12).—Another small collection like the preceding was gathered from low woods near Courtois Creek. It is a little more typical of *U. grandiflora* than the La Barque Creek population. On only one plant is the longest internode less than 150 mm. Six plants (46 per cent) have 16 or more leaves; all plants have 14 or more leaves.

Red Lake, Minn. (Chart 13).—These plants from northern Minnesota are far removed from any juxtaposition with *U. perfoliata,* and, on the chart, they tend to congregate in the upper right hand corner, as should be expected for *U. grandiflora.* However, the fact that twenty-four plants in the population (96 per cent) lack three full-length rays on the dots used to plot them indicates that in some manner they fall short of being "good grandifloras." This point is discussed following the description of the charted data.

Clarksville, Mo. (Chart 14).—The Clarksville population was collected on the upper slopes of one of the characteristic glacial knobs of southern Pike County. The plants were growing under a heavy canopy of mixed deciduous trees, with *Bidens, Hystrix, Smilacina,* and *Polygonatum.* Although the leaf indices of this population are quite low, there are only three plants (11 per cent) whose longest internode is greater than 200 mm., and only two plants (8 per cent) which, on the basis of all five characters, are "good grandifloras." These two plants are in the upper right portion of the chart.

Coxsackie, N. Y. (Chart 15).—Coxsackie is in Greene County, on the Hudson River about 22 miles south of Albany. It is therefore well within the range of *U. perfoliata.* Six plants (31 per cent) are really "good grandifloras"; that is, they are tall, have a low leaf index and a complete set of full-length rays on the chart. These six plants are, in general, in the upper right portion of the chart. The smallest plants charted tend to have higher leaf indices and incomplete ray systems; in other words, the plants in the lower portion of the chart tend to be less *grandiflora*-like than the others.

Missouri (Chart 16).—This chart depicts a synthetic population. It was constructed from material in the Missouri Botanical Garden Herbarium which had been collected in Missouri. As a rule, there is only one plant from each county. Most of the plants were not mature and fruiting; the 35 plants which were measurable are included on the chart.

These plants plot out rather well for *U. grandiflora.* Fourteen plants (40 per cent) have complete sets of rays on the dots used to plot them. The "average plant" has the longest internode, 191.4 mm., a leaf index of .372, 16½ leaves, and 1½ fruits, and is fully pubescent. With the addition of half a fruit, this rather grotesque "average plant" would make an excellent *U. grandiflora.*

This general Missouri collection averages more like *grandiflora* than the individual Missouri collections. The explanation may lie in the fact that plant collectors usually strive to collect the best specimens for herbarium material, whereas a mass collection aims for a cross-section of the population.

Billington Woods, Institute Grounds, Bloomfield Hills, Mich. (Chart 17).—This *Uvularia* population, which appears to be a single clone, covered an area of about 5 × 8 feet, and contained well over fifty fruiting stems, crowded too closely together for exact counting. The plants were growing in a moderately open place in deep, moist woods. The adjacent trees were *Ulmus fulva, Carya tomentosa, C. ovata,* and *Cercis canadensis. Osmorhiza* grew around the edge of the clone.

This population was the least *perfoliata*-like of the mass collection material. There was a high percentage of secondary and even tertiary branching. Thirteen plants (72 per cent) had more than one fruit; the average was 2.5, as many plants had 3 fruits, and a few had 4. Other averages, which reveal the *grandiflora* characteristics of the population, are as follows: length of longest internode, 200.5 mm.; leaf index, .298; total leaves, 17; pubescence, complete in all specimens.

UNCHARTED COLLECTIONS

Some smaller collections, not charted, are nevertheless noteworthy, and are listed below:

Natchitoches, La.—In 1935 Anderson noted the existence of *U. perfoliata* in a woods along Grand Ecore Road, about two miles west of Natchitoches. Natchitoches is an extension of the previously known range of *U. perfoliata* by about 400 miles. These woods range from dry to wet enough for *Taxodium* with well-developed "knees." Occasional trees bearing *Tillandsia usneoides* provide an environment contrasting strongly with that of *U. perfoliata* in New England.

Five specimens, including Anderson's and several from the herbarium of the Northwest Louisiana State Teachers College, are available for study. All have at least three leaves below the single branch. All are small plants, with few leaves. Four are too early in the fruiting stage to get much of a picture of capsule shape, or more than a general picture of the ultimate measurements. This general picture suggests, however, that these plants are remarkably "good perfoliatas." The nearest plants of *Uvularia grandiflora* are some 250 miles to the north, in central Arkansas.[2]

Monte Sano, Ala.—One plant and several fragments from the herbarium of the New York State Museum came from rich woods, over limestone, near the summit of Monte Sano in Madison County. The size and shape of the leaf are as in *U. grandiflora.* All the leaves of the pressed specimens are so thin and translucent that newspaper sub-heads can be read clearly through them. Most of the leaves are completely glabrous, those which are not glabrous are very sparsely pubescent; where *U. grandiflora* will have well over 10 hairs per sq. mm., these plants have 1 hair to about every 5 sq. mm. The pubescent specimen in Knoxville "A" was completely pubescent, and the Oakwood Park specimens with intermediate pubescence had these emergencies with the same relative density as typical *U. grandiflora.* One of the fruiting specimens from Monte Sano contained a detached flower, which may or may not have belonged to it. The inner surface of the perianth segments of this flower was smooth, as in *U. grandiflora,* but there were about three places on each segment where rudimentary papillae could clearly be seen. The population sample is too small for the formulation of any definite conclusions.

If it be possible, an even more perplexing specimen—a single sheet in the Missouri Botanical Garden Herbarium (#1267594)—from Scottsboro, Alabama—possesses characters of *U. perfoliata, U. grandiflora,* and *U. puberula.* It has leaves slightly pubescent on the dorsal surface, an extreme *perfoliata* fruit, and angles of the stem are pubescent. Furthermore, although perfoliate, the form of the plant is more like *puberula* than either of the perfoliate species.

From these rather meager data, it appears as though the perfoliate Uvularias from northern Alabama are at least as variable as the Rochester or the Knoxville populations.

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[2] A collecting trip to Natchitoches in 1951 failed to augment these with mass-collection data.

An Interpretation of the Variation in the Perfoliate Uvularias

The concept of introgressive hybridization was developed by Anderson (Anderson and Hubricht, 1938; Anderson, 1949, 1950). Introgressive hybridization, or more simply, introgression, may be defined as the inherited variation in a species which results from back-crossing an original hybrid with one parent until only a small amount of the germ plasm of the other parent remains. Frequently, the effect of so small an amount of foreign germ plasm is not immediately apparent in the mongrel offspring, and must be detected by statistical or experimental means. *Uvularia* is a perennial plant, and under the best conditions each generation will take two years to grow to flowering size. In nature, some plants—particularly those of *U. perfoliata*—apparently take even longer. Experimental hybridizations and back-crosses would have involved a prohibitive amount of time. Further, since the primary question in this investigation was whether introgression is occurring in natural populations, we adopted the statistical treatment. The charts in this paper are designed to provide critical evidence for or against the presence of extensive introgression. Theoretically, continual back-crossing to the parental species would at length produce offspring in which the effect of the foreign germ plasm was so dilute that it could be detected only by the most elaborate genetic tests, if at all.

In order to study introgression, it is valuable first to become familiar with plants in which there is reason to believe it is not a factor. This led, in the present project, to the quest for "good perfoliatas" and "good grandifloras." A study of the presumably "good" specimens led to temporary criteria for these species, such as glabrousness *vs.* pubescence, relative leafiness, relative size, branching pattern, leaf shapes, etc. With the acceptance of temporary criteria, preliminary plots of the "good" populations may be drawn up. It is important that the characters used for the ordinate and the abscissa be such that for one "good" species the values will fall in one corner of the diagram, while for the other species they fall in the opposite corner. An intimate relationship between the two species would be shown by the fact that intermediates fall at some point between the two corners reserved for the "good" species, and none in the unassigned corners of the chart. In this project, following the traditional orientation of the pictorialized scatter diagram, our charts reserve the lower left corner area for one species, *U. perfoliata*, and the upper right corner for *U. grandiflora*.

The rays on the dots are so planned that one "good" species (in this case *U. perfoliata*) should be ray-less, while the other will have a complete set of full-length rays. If the variation depicted by the rays is related, we must expect that, as the dots progress from the lower left area of the chart into the upper right, the frequency and length of the rays will tend to increase correspondingly. And if that condition appears on the chart, we cannot escape the conclusion that the condition is caused by an intimate relationship between the two species.

If introgression is a factor in the populations reproduced on the charts, what evidence for this fact appears on them? The answer reveals one of the peculiar

advantages of the pictorialized scatter diagram over other methods of data presentation for the analysis of variation. On the charts, where introgression is a factor, there is a strong tendency for the sum of the measured characters to vary together. The total variation is more cohesive than the variation of the single characters making up the total. The following examples illustrate this fact.

In a population which is varying due to some environmental factor, as of a plant which grows large and lush along a stream bank and becomes gradually smaller, less branched, etc., as it grows up a slope, the variation would be something like that in fig. 7. The dots would fall on a straight line, and the rays would all increase proportionately as the dots progressed from the lower left area to the upper right.

In introgressive populations, on the other hand (fig. 8), the position of the dots forms a spindle-shaped figure of various proportions. The only areas on the chart where no dots will fall are the two unassigned corners. As the dots progress from species "A" to species "B" the sum of the rays becomes, on the average, increasingly greater, although the progressive increase of any individual ray may appear to be a random one. Note that for any given value midway on the ordinate, the values may fall along several places on the abscissa. Further, the equally variable picture presented by the rays indicates that the mongrel examples of the population express a wide recombination of characters, just as has been found in experimental crosses and back-crosses between species and races. The tendency for any one character to correlate with the sum of the other characters is therefore greater than the tendency of a single character to correlate with that of any other single character; that is, introgression (as opposed to an environmental relationship, for example) shows recombination of characters expressed as a total tendency and not as a simultaneous correlated progression of the component characters.

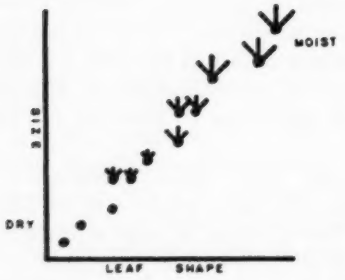

Fig. 7. A hypothetical species in which variation is due to environment. As the environment changes from moist to dry, the plant becomes increasingly small in each character. No outside genetic influence is working on the variation pattern.

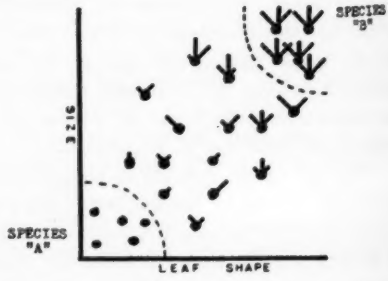

Fig. 8. Species in which introgression is causing the variation. The total ray pattern becomes greater toward the upper right-hand corner, expressing the fact that the total variation is more directional than that of any of the component characters.

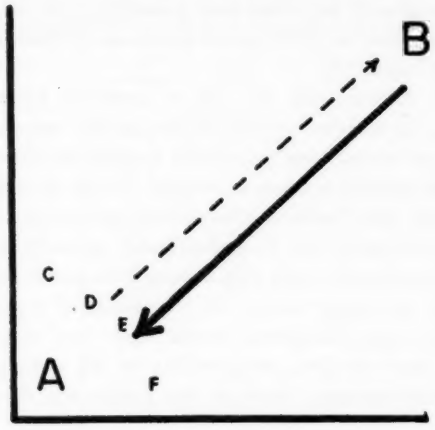

Fig. 9. See explanation below.

The ease of analyzing introgression depends upon the possible number of taxons (taxonomic entities) involved. If there are only two, the problem is simple; with three or more, it is usually very complex.

In the genus *Uvularia* there are six taxa (*U. perfoliata, U. grandiflora, U. sessilifolia, U. puberula, U. puberula nitida,* and *U. floridana*). None of these exists separated by any great distance from any one of the other perfoliate species. In some parts of the range, four taxa occur in the same geographical area. This fact raises the problem of detecting introgression between *perfoliata* and *grandiflora* without obtaining data obscured by factors originating within the taxa with which we are not presently concerned (see fig. 9, above). *Uvularia grandiflora* is markedly distinct from all the other species of *Uvularia* in a great many characters—a heavy branching pattern, multiple fruits, numerous leaves, etc. If we assign *U. grandiflora* to the upper right area of the chart, and *U. perfoliata* to the lower left area, the other four taxa might fall in a way suggested by the letters CDEF. This general picture is what we find in the present project. Actually, the four other taxa represented by CDEF, while relatively close to *U. perfoliata,* would more properly be charted in four other dimensions, although remaining in a projection of the lower left area of this chart.

In a case of this kind, we can secure valid introgression data only in the direction indicated by the solid arrow, that is, introgression of *grandiflora* into *perfoliata.* Introgression data from *perfoliata* to *grandiflora,* in the direction of the dashed arrow, would be obscured by the presence of the elements CDEF, which would come from the same direction. Because of the morphological resemblance between the various species of *Uvularia* in eastern North America, introgression of *grandiflora* into *perfoliata* is easy to detect and even, within certain limits, to

measure. Introgression of *perfoliata* into *grandiflora*, on the other hand, is so obscured by the presence of other species similar to *perfoliata* that we have no critical data for or against it.

In spite of its shortcomings, the type of statistical treatment used in this paper is superior to the standard methods of determining population averages using means, extremes, and spread, and calculating correlations from those data. The following table uses population means to describe the average plants of the fourteen field collections and three herbarium collections used in our charts. We learn little from this table except that *U. grandiflora* is generally larger than *U. perfoliata*, has a lower leaf index, more leaves, more fruit, and is pubescent as opposed to glabrous. This we already knew. If we calculated standard deviations we would discover that some populations varied more than others, and that these populations were from the area corresponding to the western boundary of *U. perfoliata*. The early statistical work in this project was done in this standard manner.

While the standard statistical procedures can and do tell us that the populations are different, and that some vary more than others, they do not tell us from whence this variation originated. The pictorialized scatter diagrams do give us this picture, subject to the restrictions outlined above.

Once the temporary criteria for "good" species are drawn up, preliminary charts may be constructed which enable us to refine our criteria to the point where the pattern of variation, if any, becomes clear. When this pattern is established, it becomes less difficult to select those characters for study which seem to express the variation pattern most clearly and to eliminate the variation which is not connected to the problem. The idea is not to construct a chart in which variation is stressed, but rather one which will express only the most essential differences between populations. If the preliminary survey of the problem indicates that introgression is not a factor in the species variation, there is no use to refine data, for no amount of data-juggling will result in a pattern which implies that introgression is a factor in the species variation.

Pictorialized scatter diagrams are just as good for demonstrating that introgression has not taken place as for showing that it has. The method was originally worked out for recording variation in fields of maize (Anderson, 1946). Begun as a purely mnemonic device, it demonstrated the importance of crosses between races of maize, and this led to its use in analyzing crosses between species of flowering plants. It is a general method of demonstrating the over-all picture in variation patterns too complex for unaided analysis. It is as useful for demonstrating the absence of character association as for its presence.

Collection	Length longest internode (mm.)	Leaf index	Total leaves	Number of fruits	Pubescence
Missouri Bot. Gard. *U. perfoliata*	95.4	.498	10.1	1.28	Absent
Missouri Bot. Gard. *U. grandiflora*	183.7	.388	15.7	1.47	Complete
Ridgewood	85.4	.506	8.9	1.06	Absent
Hawley	97.1	.461	7.4	1.00	Absent
Dyestone Creek	114.2	.560	8.2	1.00	Absent
Mountain Lake	107.1	.508	9.0	1.00	Absent
Oakwood Park	90.6	.443	8.3	1.00	Intermediate
Knoxville "A"	145.4	.431	12.4	1.05	Partial
Knoxville "B"	160.0	.346	14.2	1.06	Complete
Debbink	159.1	.352	16.3	1.12	Complete
La Barque Creek	172.0	.284	15.8	1.00	Complete
Butts	174.0	.342	15.0	1.15	Complete
Red Lake	184.1	.338	14.9	1.04	Complete
Clarksville	173.0	.306	14.5	1.08	Complete
Coxsackie	184.0	.354	15.6	1.37	Complete
Missouri Bot. Gard. "Missouri"	191.4	.372	16.3	1.50	Complete
Billington Woods	200.5	.298	16.9	2.46	Complete

Collections Giving Evidence for Charted Data

Ridgewood, N. J. (Chart 3).—Thirteen of the sixteen plants plot out as "good" *perfoliata.* There is some variation in the population, three plants having more than 9 leaves, and one with 2 fruits. While these characters tend to suggest *U. grandiflora,* there is no clear evidence that introgression has been a factor in the Ridgewood population. A 2-fruited *U. perfoliata* is atypical, but not outside the realm of normal variation for an occasional plant. If the 2-fruited plant were in an extreme position toward the *grandiflora* corner of the chart it would come under suspicion, but this is not the case.

Hawley, Pa. (Chart 4).—This is another "good" *perfoliata* population, the variation in which is mostly in the direction of larger plants with somewhat narrower leaves than is typical of *U. perfoliata.* However, since there is no concomitant increase in the ray pattern to accompany this variation, we must reject introgression in this population.

Dyestone Creek, Va. (Chart 5).—The Dyestone Creek population is composed largely of "good" *perfoliata* elements, but there is evidence that there has been some influence here from *U. grandiflora.* Of the six plants appearing highest on the internode scale, five are seen to have one or more ray fragments. On the other hand, the five plants lowest on the internode scale are devoid of rays. It then follows that the variation in this population is oriented toward *U. grandiflora* rather than simply at random. Dyestone Creek is not far from the "fringe" area in which the variation in *U. perfoliata* is so marked. There is, in fact, a suggestion in this collection of the variation pattern which will appear in the "fringe" area populations.

Mountain Lake, Va. (Chart 6).—Although west of Dyestone Creek and therefore nearer the "fringe" area, the Mountain Lake population apparently has not been influenced by introgression from *U. grandiflora.* The population contains taller plants than typical for *perfoliata,* but this may be due to environment, since there are no other connected tendencies toward *grandiflora.* There are, however, some populations in the Mountain Lake area which apparently have been influenced by introgression from *U. grandiflora.* The Mountain Lake Biological Station herbarium contains some sheets of *Uvularia,* several of which preserve what we would call "problem plants." These are occasionally identified incorrectly, but frequently they may possess some key characters of both species, and even a person familiar with the plants could conceivably be led astray. The Mountain Lake area contains plants of *U. perfoliata, U. grandiflora,* and some intermediates, as well as two other species of *Uvularia.*

The fact that our population sample does not show introgression serves to point up the fact that, even in "fringe" areas, only occasional populations display this feature. Although most of the observed intermediate populations come from "fringe" areas, it should not be implied that all fringe-area populations are intermediate.

Oakwood Park, N. Y. (Chart 7).—This population is near the western boundary of *U. perfoliata* and therefore in the "fringe" area where the greatest variation has been noted. We now can observe that this variation is due to introgressive hybridization. While the entire population consists of rather small plants, the leaves are uniformly narrower than those in Ridgewood, for example, and the picture presented by the rays shows that the *grandiflora* elements appear generally from the direction which was assigned to that species. The dots in the lower left area of the chart are generally without rays. Those in the upper right portion are all partially rayed. This is the population in which we found the intermediate pubescence. The rays are not distributed at random on the chart, but instead follow a path from the upper right, or *U. grandiflora* position. Therefore the population is intermediate because of introgressive hybridization.

Knoxville, Tenn., Collection "A" (Chart 8).—This population is really intermediate. It is located near the center of the chart, midway between *U. perfoliata* and *U. grandiflora.* In addition, the rays are more frequent and longer in the upper right portion of the plot. The plant in the lower left has a long ray to the right, indicating pubescence. While there is no doubt that this is a *grandiflora*-type pubescence, it only appeared on a portion of a single leaf and the rest of the plant was glabrous. Had we called the plant glabrous, the dot would have appeared with only a fragment of a ray off to the left, indicating a slight leafiness.

The population, essentially *U. perfoliata,* is growing in a moist area. This is not usually true for "good perfoliatas." The fact that the plants do well in this environment may be attributed to the adaptability they have acquired as a result of the introgression from *grandiflora.*

Knoxville, Tenn., Collection "B" (Chart 9).—This is essentially a *U. grandiflora* population. The picture presented by the rays presents a generally random variation. The plants average smaller than "good" populations of *U. grandiflora* should, but there is no evidence to indicate that size is not an environmental condition, or, if the result of introgression, from which small *Uvularia* the condition came.

Debbink, Wisc. (Chart 10).—These plants, like the preceding ones, are small for *U. grandiflora.* There is a slight tendency for the rays to be longer in the upper right portion of the chart than in the lower left. However, again we have no way of determining the origin of the non-*grandiflora* element which this tendency reflects, if there is actually such an element in the population.

La Barque Creek, Mo. (Chart 11).—Although variable, the variation is at random in this charted population.

Butts, Mo. (Chart 12).—The position and totality of the rays on this chart offer a faint suggestion of introgression from some non-*grandiflora* source.

Red Lake, Minn. (Chart 13).—The variation in this population with respect to *perfoliata-grandiflora* introgression is at random. Though outside the scope of this investigation, the Red Lake collection suggests strongly an introgression from *U. sessilifolia.*[3] This is reflected in the chart by the rather amorphous variation of the plots. There is no tendency toward *U. perfoliata,* in spite of the low degree of cohesiveness. This fact tends to indicate that the design of the charts has met with the demand that it reflect the *grandiflora-perfoliata* tendency without influence from other variation factors.

Clarksville, Mo. (Chart 14).—In this collection we see again a faint suggestion of introgression from a non-*grandiflora* element. There is no indication that this element is *U. perfoliata.*

Coxsackie, N. Y. (Chart 15).—The Coxsackie collection is from an area where the two species grow near to each other. While the population as a whole is quite *grandiflora*-like, there is a strong suggestion of introgression with *U. perfoliata.* This may indeed be true, but the design of the chart is such that introgression from *U. perfoliata* into *U. grandiflora* is not provable. However, since we have striven to eliminate much of the variation from directions other than that between *perfoliata* and *grandiflora* from the chart, we can state that the Coxsackie population probably represents introgression from *perfoliata* into *grandiflora.*

Missouri (Chart 16).—This synthetic population sample from herbarium sheets in the Missouri Botanical Garden reflects the general condition found in the individual Missouri collections. As a whole, these plants represent a "good" *grandiflora.* There is a slight tendency for plants with complete ray systems to be higher and farther right on the chart than those with incomplete ones, but there is no proof that this variation is from *U. perfoliata.*

[3] This suggestion is expressed by the following facts: (1) the presence of some sessile leaves on the upper portions of occasional plants; (2) the 90° angle of the primary branch, as in *U. sessilifolia,* rather than one of about 60°, as in *U. grandiflora;* and (3) the gross appearance of the plant which is similar to that of the sessile-leaved species of *Uvularia.*

Billington Woods, Mich. (Chart 17).—This is, on the whole, an excellent population of *U. grandiflora.* Of the eighteen plants, fourteen (78 per cent) have 3 rays, and of these fourteen plants (67 per cent of the total) have complete ray systems. The four plants with only two rays appear at random on the chart.

Interpretation of the Variation in the Perfoliate Uvularias

As has previously been discussed, the only clear evidence for or against introgression in the perfoliate species of *Uvularia* is from *U. grandiflora* into *U. perfoliata.* The *grandiflora* populations are often quite variable, but we cannot prove that this is due to introgression from *perfoliata.* On the contrary, we have reason, from the charted data, to believe that in many cases this is not true. The Coxsackie *grandiflora* population appears to have been influenced by introgression from *perfoliata,* and the chart indicates that this is probable, but other non-perfoliate species might be involved.

One of the most significant facts to be gleaned from the charted data is the relative rarity of introgression as a factor in the perfoliate Uvularias. We can reason that if these species hybridized easily in nature, large numbers of hybrid populations would occur throughout the area of mutual distribution. This is not so. Generally, throughout the area of overlapping distributions, each species population is distinct. Most of our typical specimens of *U. perfoliata* come from areas where *U. grandiflora* is not far away.

Once a hybrid does occur in nature, however, the way is clear for introgression to proceed. *Uvularia* is a perennial plant. It is not necessary for it to set seed each year in order to survive. Propagation is largely vegetative. The F_1 plant, then, once it occurs, can exist without genetic change (unless by mutation) for a long period of time. Since we have reasoned that these F_1 plants must be rare, it follows that at such a time as cross-fertilization occurs again in that plant, it must be between the F_1 and one or the other parent species, most likely the one closest by; in other words, a back-cross. This back-cross will resemble the parent with which the F_1 was hybridized, except that some of the characteristics of the other species may remain. In time this back-cross generation may again hybridize with the primary parent species. The cross would logically occur thus, since we have postulated that the F_1 hybridized with the parent species most adjacent to it, and the back-cross would behave similarly. Thus a second back-cross generation is formed which contains no less than seven-eighths of the characteristics of the primary parent species and no more than one-eighth of those of the secondary parent species. Genetically, it is possible to reconstitute the original species even in the first back-cross. In nature, those back-crosses with the fewest elements of the foreign species are those most likely to survive under natural conditions (Anderson, 1948). As a result of crossing between the two species, we are most likely to find back-crosses closely resembling the original primary parent species but slightly variable in the direction of the non-recurrent parent. The results of such hybridizations and back-crosses is that a genus such as *Uvularia* could persist unchanged for long periods of time, hundreds or even thousands of years.

The question then arises: Why should this condition not be prevalent throughout the areas shared in common by the two species, rather than primarily at the edge of the range of *U. perfoliata*? Away from the "fringe" areas of the specific distributions the environment is relatively uniform, and the potential parents are occupying ecological niches for which they are suited. Occasional crosses present no particular advantage to the hybrid, or they may even present something of a disadvantage with respect to the niches for which the parents have become adapted. After a time the hybrids would tend to disappear. This may have been the case with *U. flava*, the species which Smith established at the same time that he established *U. grandiflora*. *U. flava* appeared to be essentially like *U. perfoliata*, but it possessed flower characteristics like those of *U. grandiflora*. From the descriptions it appears that *U. flava*, considered rare and found "from New Jersey to Virginia," was probably an introgressive hybrid, or perhaps even an F_1, which did not add any particular advantage to the *perfoliata* element. *U. flava* apparently disappeared gradually, for the manuals of the day reflect increasing uncertainty about it until it finally was dropped into synonymy with *U. perfoliata* and was removed entirely from the literature. We have found no records of *U. flava* collections for more than sixty years, nor do we know of any botanists who claim to have seen this form in recent years.

What then is the significance of introgression as a factor in the perfoliate species of *Uvularia*? Introgression provides a reserve of adaptability on which the plant can draw, under conditions differing from those for which the parent species have become adapted. If conditions change, or if the plant migrates away from the area in which the parent species are successful, this reserve is available, with the consequence that the introgressive hybrid is more likely to be successful. The successful form differs, albeit slightly, from the parent species. Projecting this into the future, the introgressive hybrid represents a possible step in the differentiation of another kind of plant. It is the potential ancestor of a new species, which can survive and evolve in environments where the parent species would be less likely to do so. It is free to evolve to occupy a different niche than those which its relatives occupy.

The study of introgression properly belongs in the field of micro-evolution, which sheds light on a portion of the still greater field of evolution itself.

Summary

Over most of their ranges, two species of *Uvularia*, *U. perfoliata* and *U. grandiflora*, are good and distinct species. There are some populations, however, which are quite variable and possess characters intermediate between the two species. These populations are most frequent along a line roughly corresponding to the western border of the distribution of *U. perfoliata*, and this species exhibits the greatest portion of the observed variation.

It was suspected that this variation was due to introgressive hybridization. To determine whether or not this were true, extensive measurements of both the good

species and the variants were taken. Introgression is generally so subtle that special methods for its detection must be employed. These methods may be either statistical or experimental. Since *Uvularia* is a perennial, and the experimental data would involve a prohibitively long investigation, the statistical method was employed. Because of the presence of other species quite similar to *U. perfoliata*, it is shown that introgression from *perfoliata* into *grandiflora* would not be readily demonstrable, although the reverse introgression (*grandiflora* into *perfoliata*) could readily be demonstrated if it does indeed occur.

The statistical data were reduced to charts designed primarily to reveal the influence of *grandiflora* on *perfoliata*, if such influence existed. The charts demonstrate introgression from *grandiflora* into *perfoliata* in some populations.

These introgressive populations were most abundant along the western border of the distribution of *U. perfoliata*, rather than throughout its range. The introgressive populations have a survival value due to greater adaptability which enables them to be successful outside the ecological niches occupied by the parent species. When they are found in new ecological niches they will frequently persist. They may represent the beginnings of potential new varieties, which might eventually lead to new species.

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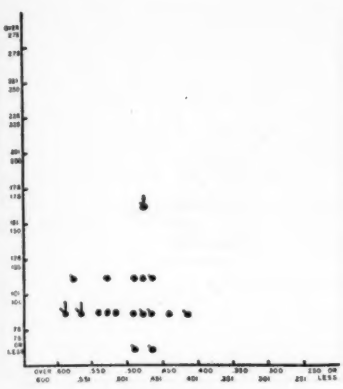

CHART 1 MBG. PERFOLIATA

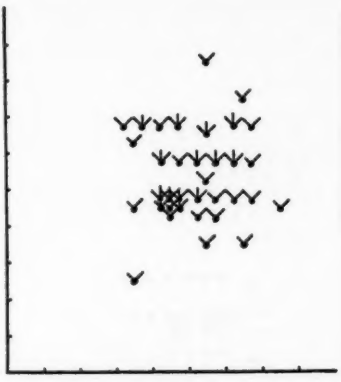

CHART 2 MBG GRANDIFLORA

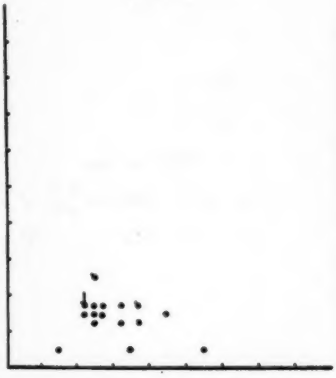

CHART 3 RIDGEWOOD

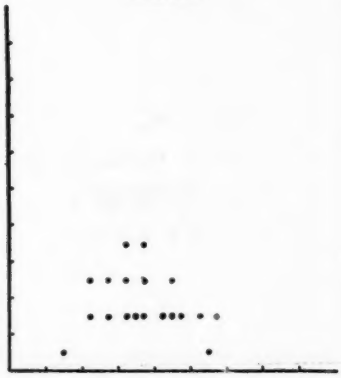

CHART 4 HAWLEY

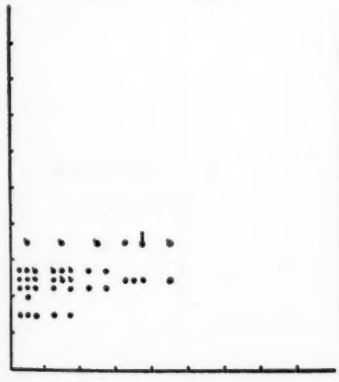

CHART 5 DYESTONE CREEK

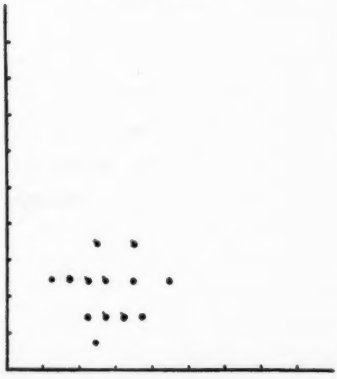

CHART 6 MOUNTAIN LAKE

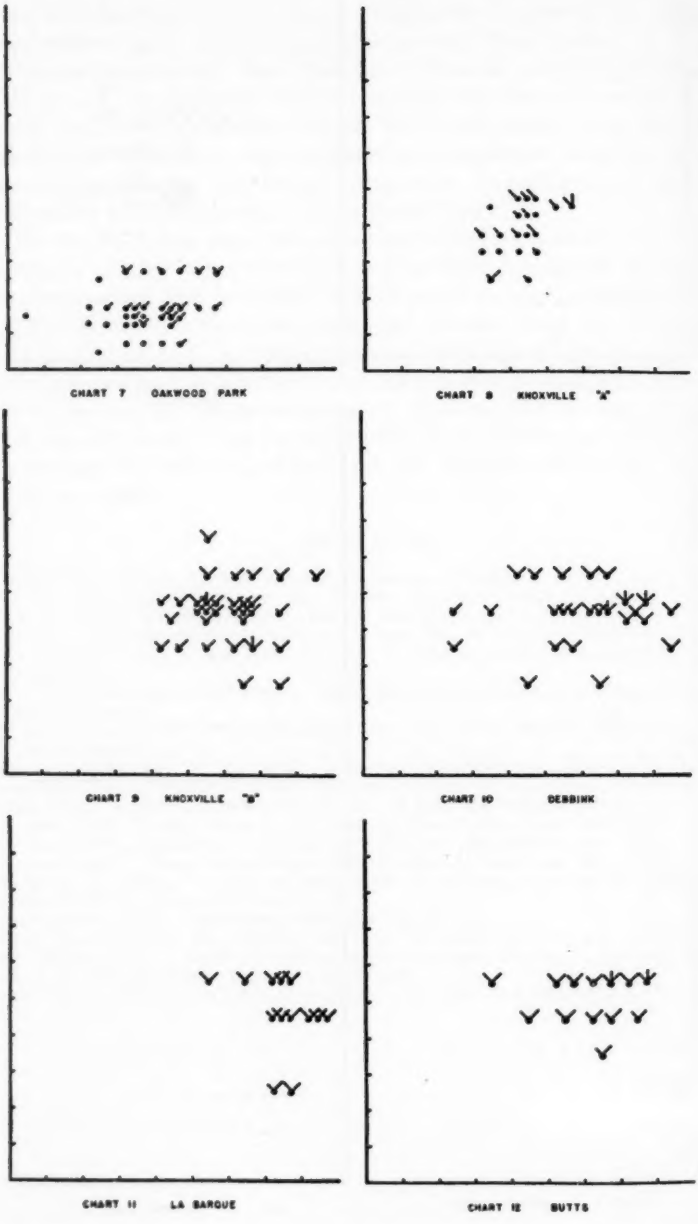
CHART 7 OAKWOOD PARK
CHART 8 KNOXVILLE "A"
CHART 9 KNOXVILLE "B"
CHART 10 DEBBINK
CHART 11 LA BARQUE
CHART 12 BUTTS

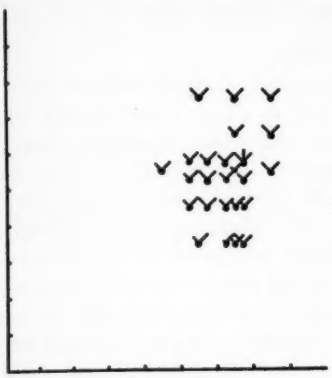

CHART 13 RED LAKE

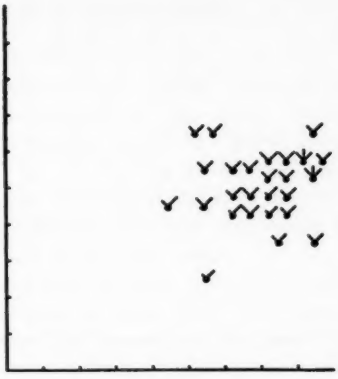

CHART 14 CLARKSVILLE

CHART 15 COXSACKIE

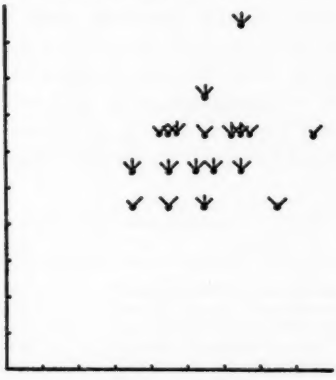

CHART 16 M.B.G. MISSOURI

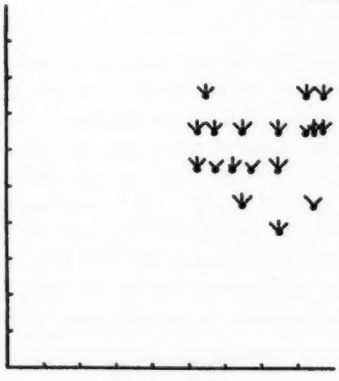

CHART 17 BILLINGTON

THE EVOLUTION OF A GRAVEL BAR

ROBERT A. DIETZ*

One of the characteristic features of many Ozark streams is the occurrence of gravel deposits usually found on the concave bank of river-bends. It has been suggested (Anderson, 1949) that these deposits, known as "gravel bars," may evolve their own flood-control systems. An investigation of one such bar on the Meramec River, at Gray Summit, Missouri, was made in order to determine how the bar had evolved physically, and, in a general sense, how this change affected and was affected by the natural populations of the river bank.

It is generally known that the size and shape of many gravel bars is not constant, but there has been no quantitative work to show this. The determination of the physical changes of this one gravel bar necessitated the assembly of all available historical data, their reduction to a common scale, and the consequent plotting of all recorded changes. This assembly of historical data is not as difficult as it might seem. There usually exist, in offices of county engineers, fairly complete surveyor's reports which may go back 100 years or more, as at the Franklin County courthouse in Union, Missouri. In addition, the field offices of the U. S. Department of Agriculture frequently have large aerial photographs of the areas within their district. Data from these two sources, as well as some private aerial photographs, were used to chart the physical evolution of the gravel bar selected. The data follow:

Record	Date	Source
Survey record	1853	Franklin County Courthouse
Survey record	1881	Franklin County Courthouse
U. S. Geol. Surv. map	1896	Supt. of Documents, Washington, D.C.
Aerial photograph	1927	Missouri Botanical Garden
Aerial photograph	1937	Department of Agriculture
Aerial photograph	1941	Department of Agriculture
Aerial photograph	1950	Made for this investigation
Survey record	1950	Made for this investigation

The records up to 1896 indicate that the Meramec River was without bends or pattern interruptions at the point where the bar is now located. These records are supported by ground reconnaisance, which reveals traces of the old river bed. The north bank of the old river stands out especially clearly (row I in figs. 1–4), marked by a ridge on which there are trees up to 6 feet DBH. The three earliest records coincide in the position of the river, indicating that it probably did not shift significantly from at least 1853 until after the data were gathered for the 1896 geological survey. The 1927 photograph shows a distinct bend of the river, with a crescent-shaped gravel bar on the concave side, as do all subsequent photographs and the 1950 survey maps (fig. 1–4). Consequently, at some time between

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1896 and 1927, the river embarked upon a period of change with meanders developing in various places.[1]

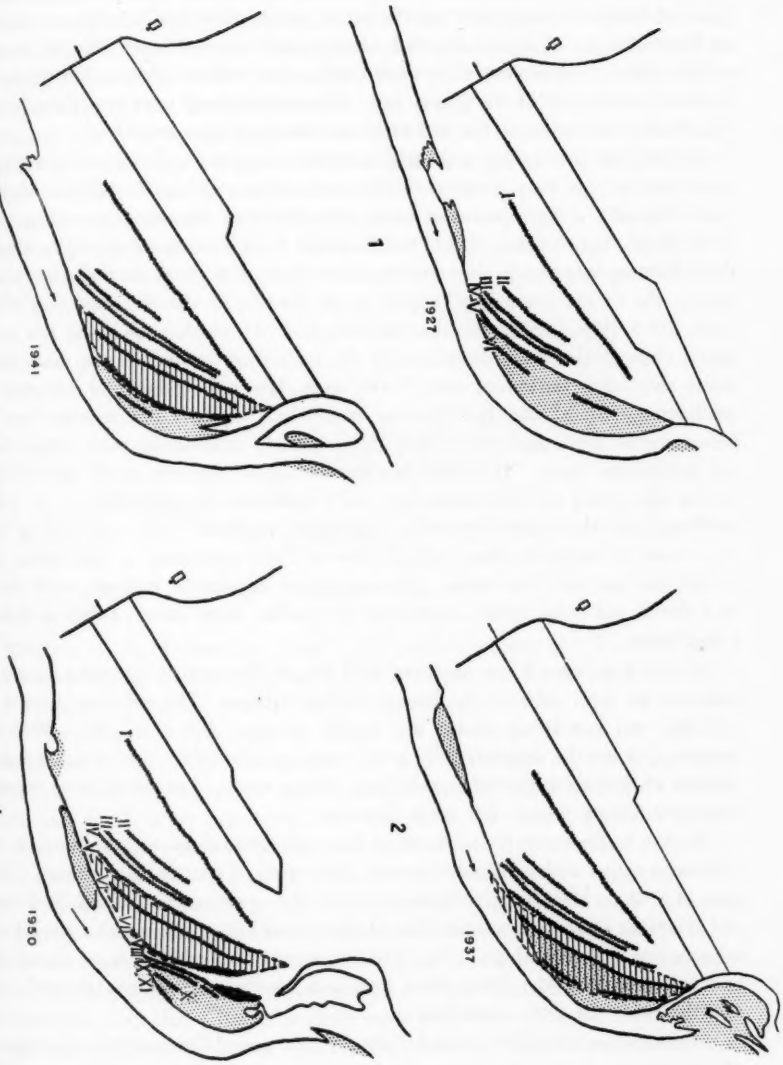
With the assembly of the data, it became necessary to reduce them to a common scale, in order to measure the changes quantitatively. An obvious solution to this problem is to photograph each reconstruction, enlarging the negatives in such a way as to establish final prints with an identical scale for each. In practice, without specialized equipment, this proved impractical. The final prints were very close to being on a common scale—within about 1 per cent—but the small differences between them made the "ground error" somewhere between 50 and 150 feet, too great for the refinement desired.

An alternate method consisted of drawing grids over the original data, with the grid lines a specified and measurable ground distance apart. Charts were then prepared with grid lines constructed equidistant on each chart. The original data were re-drawn onto the prepared charts, and were consequently on a common scale. The transferable error proved to be considerably less than the photographic error described above. Figures 1–4 are outline drawings prepared from four of the final, common-scale charts. These figures show the following facts regarding the physical changes in the gravel bar from 1927 to 1950.

The gravel bar in 1927 was about 800 feet long and 150 feet wide (fig. 1). The dark line marked with the Roman numeral I represents the line of trees along the bank of the former river-bed. In the area transect (fig. 5) these trees are marked with the key-number 12, and the remains of the river-bed with the number 11. By 1937 the bar had moved about 75 feet in a southeasterly direction, and was about 600 feet long and 200 feet wide (fig. 2). In 1941 the inland edge of the bar occupied the same position that the far bank of the river did in 1927. The downstream side of the bar remained about where it was in 1937, but the upstream portion had swung southward about 125 feet. The dimensions in 1941 were about 600 × 100 feet (fig. 3). By 1950 the shift had become nearly due east, so that the gravel bar was nearly 200 feet east of its 1927 position, and was about 500 × 110 feet in area (fig. 4). The same bar in 1952 showed marked changes since 1950. It was wider and more nearly hemispherical, and the fish-shaped bar which appears upstream in fig. 4 has extended downstream until the two bars have almost merged.

As a result of this investigation we now had available quantitative data on the physical changes of one gravel bar covering a period of twenty-three years. If we accept the supposition that the bed of the river prior to 1896 was indeed adjacent to the line of trees designated by the number I on figs. 1–4, as seems likely, then the river must have moved southward a distance of about 350 feet at the point where the upstream portion of the gravel bar was located in 1950, and

[1] Kirk Bryan (1941) proposed cycles of aggradation and degradation by the rivers of the southwestern United States. Is our cycle hololog ous with his? There are no data and we can only speculate. Etter (1949) reported an occurrence on a creek in Pike County, Missouri, which adds some fuel to such speculation.



Figs. 1–4. Dot shading shows current gravel deposits; line shading shows 1927 bar location in subsequent years. Further explanation in text.

developed a meander—on which the bar is located—back to, and a little beyond its old course in the intervening half-century or so.

Although this investigation was primarily concerned with the story of the physical change of the gravel bar, the action by the river has had a profound effect on the ecology. A critical observer on the spot, even without prior information on the spbject, can discern without difficulty that willows play an important part in the over-all story of the gravel bar. These shrubs and trees bear directly upon the physical evolution of the bar itself, and the land area behind it.

During the late spring and early summer, when the willows are in fruit, the river surface may be covered with the cottony floating seeds. Willow seeds are viable for only a short period of time, about three or four days according to the U. S. Dept. Agr. "Woody Plant Seed Manual." If conditions are right, some of these floating seeds may give rise to a new line of willows at the water's edge. Briefly, the "right conditions" appear to be these: (1) the river receding after a flood, but still slightly higher than normal, and (2) viable seeds being left on the gentle slope of the moist shore line by the retreating waters. If the seeds remain moist they may germinate, and if the river does not again flood and tear the seedlings out before they have become established, within a few months they will become small saplings. After they have become established, even severe floods fail to dislodge them. The result is a line of willow saplings at the water's edge. In the late spring of 1949 conditions were right for the establishment of willow seedlings, and the writer observed a deposition of seeds. The next spring there was a row of supple saplings, which, due to flood conditions at that time, were several feet out into the water. An attempt to dig up the saplings, with the aid of a shovel and river action, augmented by pulling from above, failed to dislodge a single one.

At the same time it was observed that the swollen stream was gouging out the substrate on both sides of the line of willow saplings. The substrate among the seedlings was not being eroded due to the cohesive action of the willow root systems, but on the contrary, the aerial stems of the willows were slowing down the rate of flow through them to the point where sand and silt were being deposited along the line on which they were growing.

As one walks away from the shore line, several lines of willows may be seen, each on a ridge, with channels between them gouged out by flood action. These lines of willows were apparently deposited in the same manner as described above, and therefore represent the shore line of the gravel bar in times past. Ring counts substantiate this hypothesis. In 1950, seven-year-old willows were found in a line approximating the 1941 shore line, and 10-year-old willows formed a line slightly inside the 1941 shore line.

Three species of willows were involved in the gravel bar studied—*Salix interior (S. longifolia)*, *Salix caroliniana (S. longipes* var. *Wardi)* and *Salix nigra*. For the last species, only one deposition occurred, apparently before 1935, but the other

two had occurred at intervals over that same period. The lines on the map (fig. 1–4) correspond to observable rows of trees. The line marked VIII was largely *S. interior,* that marked IX was largely *S. caroliniana.* Line VII contained *S. nigra, Acer saccharinum, Ulmus fulva, U. americana,* and *Populus deltoides.* Inland from line VII there were no willows. In this area the ridge furrow topography is occasionally preserved, although discerned only with difficulty. Those which are observable are marked on the illustration (figs. 1 and 4) with Roman numerals. The numbers run from I (the presumed bank of the river during the nineteenth century) to XI (the water's edge in 1950). These features tell the story of successive changes in river position since the change began. Figure 5 shows a cross-section of the area from the middle of the gravel bar northwest to the old river bank. Well-developed stream-bend gravel bars present an example of spatial succession, similar to that observed in such places as the dunes region of lower

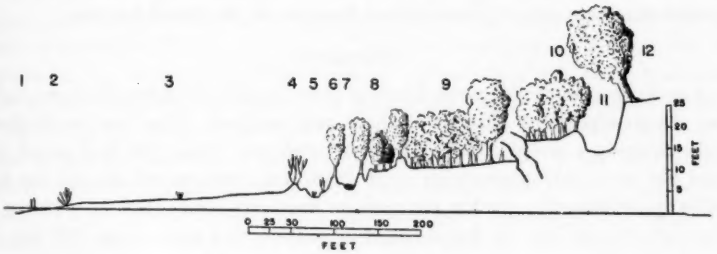


Figure 5. Explanation in the text.

Lake Michigan. In fig. 5, from the water's edge inward, we see: (1) Water Willow, *Dianthera americana,* a transient plant which is ripped out by severe floods; (2) willow seedlings of various species, the first permanent plants; (3) the strand, generally barren gravel and sand, on which the permanent plants are willows, *Amsonia illustris,* and *Panicum virgatum;* (4) and (6) ridges on which are large willows; (5) and (7) fosses or canals, gouged out by flood action, in which *Panicum* and *Amsonia* are permanent residents, as on the strand, although in the fosses they tend to slow down the flood water, resulting in the eventual filling up of these areas by deposition; (8)–(10) the area in which willows are replaced by cottonwoods, elms, and maples, roughly in that order; (11) the old river bed; and (12) the row of large old sycamores, maples, etc. making up the old river bank.

Since the three species of willows growing on this one gravel bar generally flower at different times in normal years, there are three chances during a year for conditions to be such that a line of willows could become established. Ring counts of the oldest solid line of willows (Ridge VIII) indicate that seeds for these were deposited in 1940. In the ten years from 1940 to 1949, inclusive, there were thirty chances for willows to become established. Actually, only four lines were successful, although some lines contain two species, indicating a seedling success rate of

about 13 per cent, at least as far as the establishment of a new physical line is concerned.

As previously noted, Anderson suggested that some gravel bars evolve their own flood-control systems. The writer's observations indicate that such appears to be true of the bar studied. In times of flood the water is spread out and channeled through the fosses. Those farthest from the river eventually become choked up with plants, but in the fosses of intermediate distance only such plants as *Amsonia illustris* and *Panicum virgatum* can exist through flood periods. Like the willows on the ridges, these plants are not torn out by severe floods, and they seem to serve to slow down the rate of flow in the furrows as the willows do on the ridges. More of this slowed-down, channeled water seeps into the ground, and run-off is lessened. In 1949 beaver *(Castor canadensis)* made use of one of the fosses, damming it up and creating a small pond behind it. The dam has survived several floods. By 1952 the beavers had moved on to another area, but their dam still serves to augment the other natural flood-control features of the gravel bar area.

SUMMARY

A gravel bar on the Meramec River at Gray Summit, Missouri, has been studied from the standpoint of changes in shape and location. Maps and aerial photographs covering a period of 97 years were employed. From the first record of a gravel bar on a 1927 photograph until 1950, the evolution of this bar has been studied quantitatively. It has changed in size from about 800 × 150 feet to about 500 × 110 feet. It has changed in position to a point about 200 feet east of its former location.

These changes are confirmed by an analysis of the ridges and fosses on the surface of the bar and the adjacent areas. These features are caused by the resistance of willow saplings to dislodgement when once established. This leads to the development of a ridge and fosse topography which provides natural levees and spillways for the river. Since the willows are originally laid down on the shore line, we have a record in the ridge and fosse topography of the changing shore lines over a period of years.

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